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Weed Population Dynamics in Potato Cropping Systems as Affected by Rotation Crop, Cultivation, and Primary Tillage

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WEED POPULATION DYNAMICS IN POTATO CROPPING SYSTEMS AS AFFECTED BY ROTATION CROP, CULTIVATION, AND PRIMARY TILLAGE

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By Silke D. Ullrich

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An Abstract of the Thesis Presented
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Reduction of dependence on herbicides in potato production is important to limit environmental contamination and reduce production costs. An experiment was conducted from 1992 to 1997 in northern Maine to examine the effects of two rotation crops (a green-manure mixture of oat, pea and hairy vetch vs. barley) and two tillage practices (chisel vs. moldboard) on weed population dynamics in two-year potato rotations without the use of herbicides. Chenopodium album, Gnaphalium uliainosum, and a complex of cruciferous weeds (Brassica rapa, Brassica kaber, and Raphanus raphanistrum) were dominant. Oat-pea-vetch was more weed-suppressive than barley, however, crucifer density increased in both rotations. The increase was slower with moldboard- than with chisel-plowing. Only in the last year of the study after population buildup of the crucifer

complex potato yield was reduced significantly by 27.8% due to the presence of weeds. This effect was probably enhanced by poor potato seed quality.

A simulation model of the crucifer complex population dynamics with the same treatments as the field study was developed using parameters obtained from various independent experiments and validated using the experiment above. The model incorporates detail in the depth-structure of the seedbank, seedling emergence, and size-dependent seedling mortality due to cultivations in potato. Including weather in the model by categorizing growing seasons improved model performance. In 20-year simulations variation due to weather was greater than treatment differences. Sensitivity analysis identified seed survival near the soil surface, followed by seedling survival at hilling, seedling emergence in the first week after planting (WAP) and seed production in potato years as particularly influential on the crucifer seedbank.

Simulations of contrasting weather conditions resulted in large differences in predicted population size and changes in ranking between treatments. Earlier hilling and a second hilling improved simulated weed control. Preemergence spring-tine harrowing reduced weed density more when performed 2 WAP than 1 WAP. Postemergence harrowing reduced weeds more 3 WAP than 4 WAP. To keep the crucifer population below damaging levels additional management practices need to be included in the cropping system. Further research should focus on the processes identified by sensitivity analysis and management practices acting upon them.

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1. INTRODUCTION

Modem agriculture relies heavily on herbicides for weed control. Despite the general agronomic success of chemical weed control technology, a number of undesirable side effects have gained increasing recognition. The unintended effects include the contamination of ground and surface water and the development of herbicide resistance in many weed species. Because sources of drinking water were contaminated, a number of herbicides have been banned or excluded from certain areas already (Vereijken and Van Loon, 1991). The development of new herbicides is becoming more expensive as it becomes more difficult to find herbicides with new modes of action and as environmental regulations become more strict.

As a result of these aspects of heavy reliance on herbicides, it is important to develop more environmentally sound methods of weed management. A single method on its own rarely is successful in controlling weeds sufficiently, as there is usually a number of weed species with different life cycles and survival strategies present. To achieve the desired level of overall weed control a number of methods has to be used in combination. Rotating crops with different requirements and cultural techniques, and using highly weed suppressive cover crops, mechanical weed control, and tillage practices integrated into a well designed weed management system may prevent any one weed species from being favored constantly and may allow economical weed control with reduced reliance on chemical technology (Bullock, 1992; Liebman and Gallandt, 1997).

Currently, Maine potato production relies heavily on herbicides with 98% of the area planted with potatoes treated (ERS, 1997). Traditionally, however, potatoes were considered a 'cleaning crop', because this row crop can be cultivated and hilled repeatedly resulting in quite effective mechanical weed control (Lutman, 1992). Today there are newly developed spring-tine harrows available that allow improved weed control in the crop row (Dierauer, 1992; Graf et al. 1993). Because mechanical control does not completely eliminate weeds, it is important to start with densities of germinable weed seeds in the soil as low as possible. The impact of spring-tine harrowing and hilling in potatoes on different developmental stages of the weed species present in northern Maine potato fields had not been studied before.

Most potatoes in Maine are rotated with other crops, most commonly the small grains oat or barley. Liebman and coworkers (1996) showed a close correlation between weed seed production in a rotation crop year with the germinable seedbank and weed plant density in the following potato crop. Thus even if the major economic interest in the rotation is the potato crop, weed infestation in the rotation crop phase is an important factor determining the weed pressure in the potato phase of the rotation. Consequently, for chemical-free weed management the rotation crops should be suppressive to weeds and alternative rotation crops that are likely to be highly weed suppressive should be studied. One such crop is a green-manure mixture of oat, field pea and hairy vetch that has first been studied in rotation with potato in Maine by Chucka et al. (1943). Crop mixtures have been found to be more weed suppressive than single crops in various studies as reviewed by Liebman and Dyck (1993). The crops in well chosen crop mixtures complement each other in their resource use resulting in more complete use of

the available resources and thus preempting resources from weeds (Abraham and Singh, 1984).

Two studies in Maine potato cropping systems without the use of herbicides resulted in an increase in the populations of a complex of cruciferous weed species, consisting predominantly of birdsrape mustard (Brassica rapa) but including wild radish (Raphanus raphanistrum) and wild mustard (Brassica kaber) (Liebman et al., 1996, Gallandt et al., 1998). Wild mustard can strongly reduce yields of cereal crops (Blackman and Templeman, 1938) and potato (Porter, unpublished data).

A computer simulation model was developed to increase the understanding of the factors controlling the population dynamics of these cruciferous weeds in Maine potato cropping systems. Sensitivity analysis was used to identify parameter estimates to which simulated weed populations are especially sensitive. This analysis was also used to suggest what additional experiments would be important to conduct in order to improve our understanding of the system. The simulation model can also be used to suggest methods to achieve better control of the crucifer complex.

2. IMPACTS OF ROTATION CROPS AND TILLAGE ON WEEDS INFESTING POTATO

Abstract

An experiment was conducted from 1992 to 1997 in Presque Isle, ME, to examine the effects of two rotation crops (oat (Avena sativa L.) -pea (Pisum sativum L.)-hairy vetch (Vicia villosa Roth) grown for green-manure vs. barley (Hordeum vulgare L.) grown for grain) and two plowing practices (chisel vs. moldboard) on weed population dynamics in two-year potato rotations without the use of herbicides. We hypothesized that (1) the green-manure crop mixture would be more weed suppressive than barley; and (2) that chisel-plowing would result in greater populations of weed species that produced many seeds in the season previous to tillage compared with moldboard-plowing. We also expected that there would be a shift in the weed species composition due to the newly introduced management practices at the experimental site and that weed species richness would be reduced and evenness increased in the more competitive of the rotation crops. Common lambsquarters (Chenopodium album L.), low cudweed (Gnaphalium ulininosum L.), and a complex of crucifer species (birdsrape mustard (Brassica rapa L. subsp. svlvestris (L.) Janchen) wild mustard (Brassica kaber (D.C.) L.C. Wheeler var. pinnatitida (Stokes) L.C. Wheeler), and wild radish (Raphanus raphanistrum L.)) were the dominant weed species. Weed density and biomass were consistently higher in barley than in oat-pea-vetch, except for the density of cruciferous weeds in 1996, which did not differ between rotation crops. In most years the seedbanks of total weeds and G.

uliainosum were higher in plots in rotation with barley than oat-pea-vetch. In 1995 and 1997, crucifer and total weed density were higher following chisel than following moldboard-plowing. Weed biomass in potato did not differ significantly among treatments in any year. Potato yield reduction due to weeds was only significant in 1997 (27.8%), the year with the highest crucifer complex density and biomass and poor potato seed piece quality. Both rotation crops resulted in an increase in crucifer density, however, this increase was slower with moldboard than with chisel-plowing. Future research should focus on identifying rotation crops and management practices that competitively suppress reproduction by crucifers and other fast-growing weed species.

Introduction

Weed management in modem agriculture relies heavily on herbicides. Although this approach has been effective for suppressing weeds, concerns about herbicides contaminating drinking water sources, the evolution of herbicide resistance in an increasing number of weed species, and rising costs of herbicides and other production inputs have led a growing number of farmers and researchers to seek alternative methods of weed management.

Currently, 98% of the area planted with potato in Maine and 87% of the area planted with potato in the USA are treated with herbicides (ERS, 1997). Traditionally, mechanical weed control was quite effective in potato (Lutman, 1992). However, because mechanical control does not eliminate weeds completely, it is important to minimize

densities of germinable weed seeds in the soil by using a combination of management practices.

Crop rotation is one of the management practices that can be used to reduce weeds in cropping systems (Liebman and Dyck, 1993). Potato is the major cash crop in northern Maine (MDAFRR, 1991) and is typically grown in two-year rotations. In northern Maine the choice of crops that can be grown in rotation with potato is limited mostly to summer annual species, because few crops can survive the winter. Consequently, the life cycle of annual summer weeds generally is not disrupted and they dominate the weed flora (Bridges, 1992).

Summer annual rotation crops that strongly suppress weed growth and reproduction may contribute to weed control in subsequent potato crops (Liebman et al., 1996). Barley is often planted as a grain crop in rotation with potato in northern Maine, and can compete well with weeds due to its large seed size and rapid early growth (Mohler and Liebman, 1987). Barley may also suppress weeds allelopathically (Overland, 1966; Liu and Lovett, 1993). Thus, barley is more weed suppressive than many other crops.

Mixtures of crops with complementary patterns of resource use tend to be more weed suppressive than single crops because they preempt resources from weeds resulting in lower weed biomass and density than monocrops (Abraham and Singh, 1984; Liebman and Dyck, 1993). One such crop mixture is a green-manure of oat, field pea and hairy vetch, which was first tested in Maine by Chucka et al. (1943) and found to increase potato yield compared to continuous potatoes. In the current study we wanted to compare the weed suppressive ability of barley grown alone with the oat-pea-vetch green-manure

mixture. We hypothesized that weed density and biomass would be lower in an oat-pea-vetch green-manure mixture than in a barley monocrop. We also hypothesized that germinable weed seed density in the soil would be lower in the spring following the green-manure mixture than following barley.

Primary tillage practices affect the density of weed seeds near the soil surface where a substantial proportion of seeds germinate (Grundy et al., 1996). Chisel-plowing leaves freshly shed weed seeds near the soil surface, whereas moldboard-plowing buries a larger proportion of the seeds too deep for successful seedling establishment (Cousens and Moss, 1990; Staricka et al., 1990). In field experiments (Schweizer and Zimdahl, 1984; Burnside et al. 1986) and in an analytical model (Mohler, 1993), these seed movements during tillage operations were found to result in lower weed seedling densities in moldboard than in chisel-plowed treatments after growing seasons with high weed seed production. However, when the previous growing season had low weed seed production and the field had a history of heavy weed infestations, moldboard-plowing resulted in higher weed densities than chisel-plowing. In the present study, we compared the effects of chisel- and moldboard-plowing on weed population dynamics. We hypothesized that when weed seed production was not strongly suppressed by management practices the weed species would have higher population densities in chisel than moldboard-plowed treatments. This is because its seeds would remain near the soil surface where they could germinate successfully and produce more seeds in the following year. In contrast, with moldboard-plowing, high densities of freshly shed seeds would be buried and lower densities of seeds shed in earlier years would be brought to the soil

surface. Weed species whose reproductive output was strongly suppressed should have smaller population densities in chisel than in moldboard-plowed treatments.

With a change in management practices a change in the weed community composition can be expected (Frick and Thomas, 1992; Holzner, 1978). Liebman et al. (1996) investigated weed dynamics in potato crops grown in alternate years with either oat or berseem clover in plots that were either moldboard or chisel-plowed. Over a four-year period, they found an increase in biomass of birdsrape mustard (Brassica rapa L. subsp. sylvestris (L.) Janchen), wild mustard (Brassica kaber (D.C.) L.C. Wheeler var. pinnatifida (Stokes) L.C. Wheeler), and wild radish (Raphanus raphanistrum L.), and a decrease in biomass of common lambsquarters (Chenopodium album L.), which they attributed to competition from the complex of cruciferous weed species. The present study tested whether weed community domination by cruciferous weeds would also occur when other crops were grown in rotation with potato.

Clements et al. (1994) suggested that fewer weed species are able to survive within a competitive crop than within a crop with lower competitive ability. Consequently, we hypothesized that the number of weed species present in an oat-pea-vetch green-manure mixture would be less than in a barley monocrop (i.e., weed species richness would be reduced). We also hypothesized that the reduced weed species richness in oat-pea-vetch would be accompanied by a more equitable balance of weed species within the community (i.e., weed species evenness would be increased). Mohler and Liebman (1987) found that the dominant weed species in their experiment were more affected by crop competition than were the other weed species present, resulting in greater equitability in the most weed suppressive crop.

With changes in crop rotation and tillage practices we expected to see changes not only in weed density and biomass, but also in potato performance. Specifically, we hypothesized that potato yield reduction due to weeds would increase as weed density and biomass increased. To test this and other hypotheses mentioned previously, we conducted a field experiment in which potato was grown in alternate years with two rotation crops (barley grown for grain or oat-pea-hairy vetch grown for green-manure) and with two contrasting tillage practices (moldboard- or chisel-plowing). Weed seed and weed plant densities and biomass were monitored over a six-year period in the same field to determine the effects of the management practices on weed dynamics.

Materials and Methods

Site and Experimental Design

The experiment was conducted from 1992 to 1997 on a Caribou gravely loam (coarse-loamy, mixed, frigid Typic Haplorthods) at the Maine Agricultural and Forest Experiment Station's Aroostook Farm in Presque Isle, Maine. The field was previously farmed conventionally for many years and had been planted with a sequence of potato, oat, and grass/clover hay. The field was planted with oat in 1991, and was moldboard-plowed and harrowed in September 1991 before the start of the experiment. The soil was limed to reach a pH of 6.0 according to University of Maine Plant and Soil Analytical Laboratory recommendations, after pH determination for the top 20 cm in 1: 1 soilwater slurry. Soil organic matter was determined via loss on ignition at 538" C in 1993 and 1994 and at 371" C from 1995 to 1997. The higher temperature method generally

produces organic matter estimates that are 0.5 to 1.0 g kg^{-1} higher than the lower temperature method (Hoskins, 1995). Mean soil organic matter content was 4.6 g kg^{-1}. Mean available phosphorus level in the surface 20 cm of soil was 29 kg ha^{-1}; available potassium level was 3 18 kg ha^{-1} (Table 2.1). Both P and IS were determined via extraction with pH 3.0, 1 M NH_4Ac solution and inductively coupled plasma emission spectroscopy. Weather data were obtained daily at a distance of about 1 km from the experimental site.

Table 2.1. Soil test results for field site at Presque Isle, ME.
Soil sampled in the spring before application of fertilizers.

Year	pH (in water)	OM † loss on ignition g kg^{-1}	P§	K ‡	Mg	Ca	CEC§
			kg ha^{-1}				me $100g^{-1}$
1992	5.5	n.d.¶	27.3	314	278	1066	9.2
1993	5.8	4.1	26.3	278	367	1263	4.5
1994	5.6	4.6	30.9	324	438	1478	6.6
1995	6.1	4.8	29.6	297	678	1818	6.9
1996	5.6	4.9	30.6	298	576	1534	9.2
1997	6.4	--	29.6	401	606	2250	7.7
mean	5.8	4.6	29.0	318	490	1568	7.4
SD	0.4	0.4	1.8	43	154	420	1.8

† organic matter (OM) loss on ignition
‡ estimate of plant available potassium
§ CEC ▪ cation exchange capacity
¶ n.d. ▪ not determine

The experiment was conducted over three cycles of a two-year rotation with potato planted in alternate years (1993, 1995, and 1997). A completely randomized split-plot design with three factors and four replications was used. The main-plot factor was

tillage: chisel versus moldboard-plowing. Sub-plots consisted of a 2 x 2 factorial combination of rotation crops (barley grown for grain versus an oat-pea-vetch green-manure mixture) and weed infestation level (weeds remaining after cultivations versus supplemental hand-weeding). The latter factor was included to determine rotation crop and tillage effects on potato yield in the absence of weeds, and to determine weed-related potato yield loss. Subplot units were 4.6 m x 7.6 m. The main plots consisted of four subplots in a row in the direction of their long sides, with 4.6 m alleys between subplots to prevent transfer of residues and weed seeds. All tillage and cultivation operations were performed along the length of these main plots. The width of the subplots corresponded to five rows of potato.

Rotation Crop Management

After moldboard-plowing and harrowing in September 199 1, the seedbed was prepared with a field cultivator on 2 1 May 1992 and the crops were planted the following day. In 1994, seedbed preparation was on 3 June and planting on 4 June, whereas in 1996 the seedbed was prepared and the crops planted on 28 May. In 1992 and 1994 'Robust' barley was planted at 135 kg ha-'; in 1996 the barley seeding rate was 112 kg ha-'. Barley was planted using a grain drill and supplied at planting with 40 kg N ha^{-1} as ammonium nitrate. In 1992, the green-manure mixture was planted with 'Porter' oat (35 kg ha-'), 'Columbia' field pea (170 kg ha^{-1}), common hairy vetch (35 kg ha-'), and berseem clover (11 kg ha^{-1}). Pea, hairy vetch and clover were inoculated with appropriate strains of Rhizobium. In 1994 and 1996, the seeding rate for oat was increased to 54 kg ha-', the

pea variety was changed to 'Trapper' and berseem clover was omitted, but hairy vetch seeding practices remained unaltered. In each year, oat and pea were planted with a grain drill, and hairy vetch was sown in the same operation from additional boxes on the grain drill. Subsequently the entire field was packed with a roller. No weed, insect pest, or disease control measures were applied after planting during the rotation crop phases of the experiment. Barley was harvested for grain at maturity and the straw remained on the plots. The green-manure remained in the plot and was winterkilled, except for a few surviving hairy vetch plants. Both barley straw and the green-manure residue were incorporated into the soil the following spring before planting potato.

Potato Management

Prior to planting potato, rotation crop residues were cut up by disking and then plowed according to the assigned tillage treatments. Tillage dates were 20 May 1993, 19 May 1995, and 4 June 1997. Chisel-plowing was done with a John Deere Model 710 'Soil Saver' with 7 standards (spaced 38 cm apart) equipped with 10 cm wide, twisted shovels set to till to a depth of 30 cm'. Moldboard-plowing was done with a John Deere Model 4200 three-bottom, two-way plow in 1993 and 1995 and a five-bottom non-reversible plow in 1997. Both types of moldboard-plow were set to till to a depth of 25 cm. Seedbeds were then prepared by disking and spring-tooth harrowing. Potato (cv. 'Atlantic') was planted as whole seed pieces in 1993 and 1995 and as cut seed pieces in

[1] Mention of any product is for scientific purpose only and does not imply that the named product is better or worse than any other brands available.

1997. The quality of the cut seed pieces in 1997 was poor resulting in poor potato emergence. Mean potato plant density in 1997 was only 2.6 plants m^{-2}, compared to 4.3 plants m^{-2} in 1995; in 1993 potato plant density was not determined, but the stand appeared normal (M. Liebman, personal observation, 1993). Rows were 91 cm apart and potato pieces were placed 23 cm apart within rows. Fertilization consisted of 172 kg ha^{-1} of N, P_2O_5 and K_2O each, applied at planting in two bands on either side of the row.

In 1995 and 1997, all plots were harrowed with a Lely spring-tine harrow, 16 and 8 days after planting, respectively, i.e. shortly before potato emergence. In 1995, the setting of the harrow did not force the spring-tines into the soil sufficiently to break the crust of the dry soil consistently and the driving speed was 9.4 km h^{-1}. In 1997, the spring-tine harrow was set more aggressively and broke up the soil crust at a driving speed of 12 km h^{-1}.

In all years with potato, all plots were cultivated with S-tines between the rows about 24 days after planting (DAP) when potato plants were about 1 O-l 5 cm tall. In 1993, this cultivation was combined with shallow working metal fingers over the rows. Subsequently the potato crop was hilled twice with a spade hiller first between 29 to 39 DAP and again one to two weeks later. Weed-free plots were hand-weeded weekly starting at potato emergence.

The potato plant tops were shredded with a rotobeater in early September. Harvest followed about two weeks later on 17 September 1993, 18 September 1995 and 24 September 1997.

Colorado potato beetle infestations were managed using economic threshold levels recommended by University of Maine Cooperative Extension (Dwyer et al., 1994).

Bacillus thuringiensis subsp. kurstaki strain eg2424 (BTk) was sprayed when threshold levels for 1 st and 2nd instar (small) larvae were exceeded in 1993 and 1995. When the threshold for 3rd and 4th instar (large) larvae or adults was exceeded, rotenone (Rotacide®5EC) with piperonyl butoxide (PBO) was applied at recommended rates. In 1997, Bacillus thuringiensis subsp. tenebrionis (BTt) and Beauveria bassiana strain RS252 were applied when the threshold for small larvae was exceeded; large larvae and adults never exceeded thresholds.

Diseases were managed according to recommendations of University of Maine Cooperative Extension (Dwyer et al., 1994) using minimum rates and longest recommended spray intervals. Mancozeb was used in 1993, whereas in 1995 and 1997 copper hydroxide was applied.

Sampling

All sampling was performed within the central 2.5 m x 4.5 m of the subplots to avoid edge effects. The weed seedbank was sampled after tillage and seed-bed preparation, but before planting the crops. Five soil cores (10 cm depth and 8.3 cm diameter) were drawn from each subplot. All samples from an individual subplot were combined and sieved through a 6.5 mm screen mesh to remove rocks. The content of germinable weed seeds in the soil was then determined using a greenhouse germination method, adapted from Gross (1990) and Forcella (1992). The soil was spread in flats on top of 3 cm of wetted fine vermiculite, which was used to buffer soil moisture. The depth of soil in the flats was 2 cm or less. From 1992 to 1996 the flats were watered as needed

(2 or 3 times a day) with a misting nozzle, whereas in 1997 an automatic misting system was used that watered the flats every 4 h for 2 minutes, from 30 minutes after sunrise until sunset. Emerging weed seedlings were identified, counted by species, and removed regularly. Every four weeks the flats were allowed to dry, after all seedlings had been counted or transplanted into pots for later identification. The dry soil was then crumbled, mixed and rewatered. Four such germination cycles of about four weeks each were completed each year. This method of greenhouse germination does not reveal the complete content of the soil seedbank (Gross, 1990). Its sole objective in this study was to measure the readily germinable weed seedbank, i.e. the potential for weed seedling recruitment in the field.

Weed biomass and density in the rotation crops were sampled in two randomly chosen 0.5 m^2 quadrats per subplot. All plants were cut with scissors at the soil surface on 2 1 August 1992, 15 August 1994, and 22-23 July 1996. The cut plant material was then sorted and counted by species. All plants of an individual species were combined, dried at 70" C for several days, and weighed.

In potato phases of the experiment, weeds were cut at the soil surface in two randomly selected 0.5 m^2 quadrats per subplot in 1993 and in four 0.25 m^2 quadrats in 1995 and 1997. The sampling dates were 12 August 1993, 1 August 1995 and 7 August 1997, after all cultivation and hilling operations were completed. The quadrats were as wide as the potato rows and centered over the row. The weeds were then sorted, counted and weighed as above for the rotation crops.

Weed species richness (S) and evenness (E) were determined from the weed plant density data, with S = number of species present and $E = (-\sum p_i \ln p_i) / \ln S$, where p_i = the proportion of the sample belonging to species i (Magurran, 1988).

Potato yield was determined in 3.05 m long sections of two central rows in each subplot. Tubers were lifted mechanically with a two-row digger and hand picked into bags. After about one month of storage, the potato tubers were graded by subplot. Decayed and externally defective tubers were removed and the remaining tubers were sorted and weighed by size class. US #1 yield was calculated as marketable tubers from 48 to 102 mm diameter.

Statistical Analysis

The data were subjected to analysis of variance using the MGLH procedure of Systat for Windows 7.0 (SYSTAT, 1997). For potato tuber yields and weed plant density and biomass in 1992 (before tillage and hand-weeding were implemented), the data from all 32 subplots were analyzed. For weed seedbank, density, and biomass responses, only data from the 16 non-hand-weeded subplots were used in the analysis. The ANOVA models included terms for tillage system, rotation crop, weed infestation and their interactions. Tillage system effects were tested against the 'replication nested within tillage' term; all other effects were tested against the residual error. To meet the ANOVA assumption of homogeneity of variance, weed density and weed seedbank data were subjected to a $\sqrt{(x+1)}$ transformation, and biomass data were subjected to a $\log_e(x+1)$ transformation. Potato yield data met ANOVA assumptions without transformation.

Coefficients of variation were determined using formulae provided by Steele and Torrie (1980, p. 385).

The trends of weed population dynamics over years were analyzed using repeated measures analysis provided in the general linear model procedure of Systat 7.0 (SYSTAT, 1997). Single-degree of freedom polynomials were protected by either significant Greenhouse-Geiser and Huynh-Feldt epsilon in the univariate summary test or significant multivariate repeated measures analysis for each factor; when a significant polynomial trend was not protected by one of the above, Bonferroni adjustment of the significance level was performed. When significant three-way interactions (year x tillage x rotation crop) were identified in the repeated measures analysis, linear regressions (for a significant interaction in the linear trend) or nonlinear regressions of the quadratic polynomial model (for a significant interaction in the quadratic trend) were performed for each individual treatment using Systat 7.0. The parameter estimates for the linear term in the linear regressions and for the quadratic term in the nonlinear regressions of quadratic polynomial trend were compared pair-wise (Zar, 1996) using the following test:

$$t = (\beta_1 - \beta_2) / \sqrt{(SE_{\beta 1}^2 + SE_{\beta 2}^2)} \qquad (1)$$

β_1 and β_2 are the point estimates of a parameter in the regression and $SE_{\beta 1}$ and $SE_{\beta 2}$ the standard errors of these point estimates. The subscripts 1 and 2 represent two different treatment combinations.

Results and Discussion

The dominant weed species present in the field were C. album, G. uliginosum, and a complex of cruciferous species, consisting mostly of B. rapa, although some plants of R. raphanistrum and B. kaber were also present. In the following analyses the latter three species are called the 'crucifer complex', because they have a fairly similar ecology and cannot be distinguished readily in the seedling stage. The crucifer complex and C. album often cause yield losses in potato and crops in rotation with potatoes in Maine (Bridges, 1992). All remaining species were less numerous (< 28.3% of plant density and < 12.1% of seed density). They will be discussed only in the context of rotation crop effects on weeds and are referred to as 'other weeds'.

Rotation Crop Effects

Total weed density, the densities of two of the most numerous weed species, C. album and G. uliginosum, and the density of 'other weeds' were significantly lower in the crop mixture of oat, pea, and hairy vetch than in the barley monocrop in all three rotation cycles (Table 2.2). Only the 'crucifer complex' did not follow this pattern consistently. In 1994, density of the 'crucifer complex' was significantly lower in oat-pea-vetch than in barley, but in 1992 and 1996, no significant differences were detected. In 1992, crucifer density was highly variable (CV = 1 01 . 1%), making detection of small differences unlikely. The first half of the season in 1996 was wet and cold (Table 2.3), which was apparently favorable for growth and survival of the 'crucifer complex', regardless of rotation crop species.

In 1992 and 1994, all weeds produced significantly more biomass in barley than in oat-pea-vetch (Table 2.4). In 1996, all weeds except the 'crucifer complex' also produced significantly more biomass in barley than in oat-pea-vetch. The 'crucifer complex' produced much more biomass in 1996 than in the previous rotation crop years. Total weed biomass was dominated by the 'crucifer complex' in 1996 and was not significantly different between the two rotation crops.

Overall, oat-pea-vetch had a strong competitive effect on most weed species in the study. Pea and oat formed a dense canopy early in the season and probably outcompeted most weed species for light. Hairy vetch grew rapidly after pea and oat senesced and filled in gaps which likely led to late-season weed suppression. Thus the response of C. album, C. uliginosum and other weed species, with the exception of the 'crucifer complex' in 1996, to the rotation crops supports the hypothesis that crop mixtures are more weed suppressive than monocrops.

However, this general trend did not apply in the case of the 'crucifer complex' in 1996. The weeds of the 'crucifer complex' have a very high initial growth rate and mature early, enabling them to keep up with the growth of pea and stay at the top of the crop canopy until they mature in some years. Mohler and Liebman (1987) reported that B. kaber matured synchronously with pea and was affected very little by the presence of that crop. It might be possible to increase weed-suppression by the oat-pea-vetch green-manure mixture by increasing pea seeding rates which results in earlier canopy closure in

Table 2.2. Weed density in rotation crop years as affected by rotation crop and tillage.

Tillage system	Rotation Crop	Weed number per m^2 1992	1994	1996		year effect polynomial trends linear	quadratic
				Chenopodium album			
chisel	oat/pea/vetch	47	8	44	†		
chisel	barley	150	86	117			
moldboard	oat/pea/vetch	47	8	51			
moldboard	barley	150	76	84			
				ANOVA (p)‡			
					Year	NS	0.008
Tillage (T) effect		--§	NS¶	NS	Year x T	NS	NS
Rotation crop (R) effect		0.012	0.001	0.023	Year x R	NS	0.027
TxR effect		--	NS	NS	Year x T x R	NS	NS
CV_T, %		--	30.2	34.7			
$CV_{R \text{ and } TxR}$, %		56.2	36.3	22.4			
				Crucifer Complex			
chisel	oat/pea/vetch	13	21	96	†		
chisel	barley	16	58	77			
moldboard	oat/pea/vetch	13	28	103			
moldboard	barley	16	51	119			
				ANOVA (p)‡			
					Year	<0.001	0.055
Tillage (T) effect		--§	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		NS	0.013	NS	Year x R	NS	0.052
TxR effect		--	NS	NS	Year x T x R	NS	NS
CV_T, %		--	24.5	23.8			
$CV_{R \text{ and } TxR}$, %		101.1	25.1	18.6			
				Gnaphalium uliginosum			
chisel	oat/pea/vetch	4	0.0	43			
chisel	barley	576	122	347			
moldboard	oat/pea/vetch	4	2	39			
moldboard	barley	576	142	273			
				ANOVA (p)‡			
					Year	0.010	<0.001
Tillage (T) effect		--§	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		<0.001	<0.001	0.001	Year x R	0.003	<0.001
TxR effect		--	NS	NS	Year x T x R	NS	NS
CV_T, %		--	30.9	20.8			
$CV_{R \text{ and } TxR}$, %		16.5	31.1	33.3			
				other weeds			
chisel	oat/pea/vetch	9	9	105	†		
chisel	barley	66	118	155			
moldboard	oat/pea/vetch	9	17	46			
moldboard	barley	66	116	104			
				ANOVA (p)‡			
					Year	<0.001	NS
Tillage (T) effect		--§	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		<0.001	<0.001	0.041	Year x R	NS	0.024
TxR effect		--	NS	NS	Year x T x R	NS	NS
CV_T, %		--	29.1	22.2			
$CV_{R \text{ and } TxR}$, %		36.0	12.3	25.4			
				Total Weeds			
chisel	oat/pea/vetch	73	38	294	†		
chisel	barley	808	384	695			
moldboard	oat/pea/vetch	73	55	239			
moldboard	barley	808	385	579			
				ANOVA (p)‡			
					Year	NS	<0.001
Tillage (T) effect		--§	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		<0.001	<0.001	<0.001	Year x R	0.001	0.008
TxR effect		--	NS	NS	Year x T x R	NS	NS
CV_T, %		--	24.2	13.2			
$CV_{R \text{ and } TxR}$, %		20.0	6.7	10.9			

† means presented are untransformed

‡ ANOVA for individual years was performed on $\sqrt{(x+1)}$ transformed data. Repeated measures ANOVA for polynomial trends over years was performed on untransformed data.

§ tillage treatments were initiated in 1993.

¶ NS - nonsignificant at $p > 0.1$.

Table 2.3. Average air temperature and precipitation at Aroostook Farm, Presque Isle, ME.

	month				Season	month				Season
	May	June	July	Aug.	Average	May	June	July	Aug.	Total
	Average Air Temperature [°C]					Precipitation [mm]				
1992	12.1	16.7	16.8	18.3	15.7	38	107	94	128	419
1993	11.3	16.3	18.8	19.1	15.7	83	141	51	76	482
1994	10.0	18.3	21.1	17.7	16.8	115	118	81	32	345
1995	11.2	18.3	21.3	20.6	17.9	58	39	61	61	219
1996	10.1	16.8	18.8	18.9	16.2	101	93	130	65	390
1997	9.7	17.2	19.7	17.6	15.5	138	62	74	111	449
30 year average (1967-97)	11.1	16.6	19.3	18.1	16.3	85	86	94	101	365

Table 2.4. Weed biomass in rotation crop years as influenced by rotation crop and tillage.

Tillage system	Rotation Crop	Weed biomass [g m^{-2}] 1992	1994	1996		year effect polynomial trends linear	quadratic
				Chenopodium album			
chisel	oat/pea/vetch	5.7	3.8	4.2	†		
chisel	barley	16.0	24.1	16.1			
moldboard	oat/pea/vetch	5.7	21.4	6.1			
moldboard	barley	16.0	20.8	13.0			
				ANOVA (p)‡			
					Year	NS§	0.007
Tillage (T) effect		--¶	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		0.012	0.016	0.012	Year x R	NS	NS
TxR effect		--	NS	NS	Year x T x R	NS	NS
CV_T, %		--	30.4	38.0			
$CV_{R \text{ and } TxR}$, %		42.6	26.2	24.4			
				Crucifer Complex			
chisel	oat/pea/vetch	4.1	0.6	62.8	†		
chisel	barley	14.1	5.0	64.8			
moldboard	oat/pea/vetch	4.1	3.3	49.2			
moldboard	barley	14.1	3.5	79.1			
				ANOVA (p)‡			
					Year	<0.001	0.008
Tillage (T) effect		--	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		0.048	0.047	NS	Year x R	NS	NS
TxR effect		--	NS	NS	Year x T x R	NS	NS
CV_T, %		--	56.1	10.7			
$CV_{R \text{ and } TxR}$, %		70.8	70.2	14.8			
				other weeds			
chisel	oat/pea/vetch	2.5	0.6	1.4	†		
chisel	barley	7.9	5.3	3.8			
moldboard	oat/pea/vetch	2.5	4.1	0.3			
moldboard	barley	7.9	3.8	2.9			
				ANOVA (p)‡			
					Year	0.002	0.010
Tillage (T) effect		--	NS	0.083	Year x T	NS	NS
Rotation crop (R) effect		<0.001	0.016	0.005	Year x R	0.007	0.015
TxR effect		--	NS	NS	Year x T x R	NS	0.071
CV_T, %		--	50.7	29.3			
$CV_{R \text{ and } TxR}$, %		53.0	49.9	41.3			
				Total Weeds			
chisel	oat/pea/vetch	12.3	5.1	68.8	†		
chisel	barley	38.1	34.3	83.9			
moldboard	oat/pea/vetch	12.3	28.8	55.6			
moldboard	barley	38.1	28.1	95.4			
				ANOVA (p)‡			
					Year	<0.001	0.006
Tillage (T) effect		--	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		<0.001	0.008	NS	Year x R	NS	NS
TxR effect		--	0.083	NS	Year x T x R	NS	<0.1
CV_T, %		--	22.3	9.8			
$CV_{R \text{ and } TxR}$, %		19.4	20.4	12			

† means presented are untransformed.

‡ ANOVA for individual years was performed on $\sqrt{(x+1)}$ transformed data. Repeated measures ANOVA for polynomial trends over years was performed on untransformed data.

§ NS - nonsignificant at $p > 0.1$.

¶ tillage treatments were initiated in 1993.

oat-pea-vetch green-manure mixtures (Jannink et al., 1996). High pea densities also increase the risk of lodging (Pullman and Hebblethwaite, 1990), which may enhance a crop's ability to suppress weeds as the lodging crop presses most weeds underneath it to the ground, where they rot (S. Ullrich, personal observation, 1994 and 1996).

The tendency towards better weed suppressive ability of oat-pea-vetch, as compared with barley, might not hold under all environmental and crop production conditions. None of the years in which rotation crops were sown during the course of this study were very dry. The effect of the rotation crops on the weeds, however, could be reversed in a dry year, as barley has been reported to be a much stronger competitor with weeds for water than pea (Mohler and Liebman, 1987). The addition of one or two passes with a spring-tine harrow in barley could reduce weed infestations in this crop considerably (Rasmussen, 1992).

Fertilizer regime is another factor that might have contributed to the difference in weed infestation between the rotation crops. Barley was supplied with fertilizer at planting, whereas oat-pea-vetch did not receive any fertilizer. C. album germination, for example, can be stimulated by the presence of nitrate (Williams and Harper, 1965). Many fast-growing and competitive weed species may benefit more from the application of broadcast fertilizer than associated crops (Di Tomaso, 1995).

In 1993, after only one year in rotation crops, G. uliginosum and total germinable weed seed density were significantly lower in plots following oat-pea-vetch than in plots following barley (Table 2.5). The same effect was observed in the two following rotation cycles in 1995 and 1997. Such an effect could not be detected for C. album, probably because this species had a high seed density in the soil at the site of the experiment at the

beginning of the study (Table 2.5). Seeds of this species have high rates of dormancy and can remain viable in the soil for many years (Kolk, 1962), thus covering any effects of recent changes in seed input with the large seed pool that was already present in the field. Of all species present in this study, the 'crucifer complex' showed the least difference in density and biomass production between the two rotation crops. No significant rotation crop effects on the seedbank of this species complex could be detected.

Tillage Effects

Significant effects of the tillage treatments on weeds could be observed only in years in which potato was grown (Tables 2.5 and 2.6). Those were the years in which plowing was conducted. One year after each tillage operation, i.e., in the rotation crop years, no significant tillage effects were detected (Tables 2.2 and 2.4).

In 1993, following the first primary tillage operation, no significant tillage effects were observed. However, there were significantly more 'crucifer complex' weeds in potato after chisel than after moldboard-plowing in 1995 and 1997 (Table 2.6). In 1995, there was a trend towards higher total weed density in chisel than in moldboard-plowed plots. In the third potato crop (in 1997), this became a statistically significant effect in the same direction (Table 2.6). These patterns are similar to those observed by Schweizer and Zimdahl (1984), Burnside et al. (1986), and Mohler (1993) for situations in which high weed seed production occurred. Only in 1997, after the third tillage event and population buildup of the 'crucifer complex' had occurred, did primary tillage practices

Table 2.5. Germinable weed seedbank in the spring at planting as affected by rotation crop and tillage practice.

Tillage system	Rotation crop	1992	1993#	1994	1995#	1996	1997#		polynomial trends: linear	quadratic	cubic	quartic
		Weed seed density in number per m^2 to 10 cm depth										
							Chenopodium album					
chisel	oat/pea/vetch	3755	3560	1263	607	812	784	†				
chisel	barley	3045	2535	1917	1129	1297	1147					
moldboard	oat/pea/vetch	3810	3251	1104	1306	989	1688					
moldboard	barley	5885	3763	2580	1493	914	1744					
			ANOVA (p) on √ (x+1) transformed data						ANOVA (p) on untransformed data?			
								Year	0.001	0.010	NS‡	NS
Tillage (T) effect		--§	NS‡	NS	NS	NS	NS	Year x T	NS	NS	NS	< 0.100
Rotation crop (R) effect		NS	NS	0.020	NS	NS	NS	Year x R	NS	NS	NS	NS
TxR effect		--	NS	NS	NS	NS	NS	Year x T x R	NS	NS	NS	NS
CV_T %		--	48.4	34.3	37.3	31.1	29.6					
$CV_{R \text{ and } TxR}$ %		47.2	24.1	19.2	25.1	25.6	41.9					
							Crucifer Complex					
chisel	oat/pea/vetch	206	424	813	745	616	1940	†		a ¶		
chisel	barley	140	80	300	252	215	1250			ab		
moldboard	oat/pea/vetch	458	247	406	177	597	644			ab		
moldboard	barley	103	221	601	429	354	373			b		
			ANOVA (p) on √ (x+1) transformed data						ANOVA (p) on untransformed data			
								Year	<0.001	0.016	0.011	0.009
Tillage (T) effect		--§	NS	NS	NS	NS	0.026	Year x T	0.025	NS	0.021	0.031
Rotation crop (R) effect		NS	NS	NS	NS	NS	NS	Year x R	NS	NS	NS	NS
TxR effect		--	NS	NS	0.051	NS	NS	Year x T x R	NS	0.041 ‡	NS	NS
CV_T %		--	64.0	34.5	39.8	34.7	29.4					
$CV_{R \text{ and } TxR}$ %		17.3	57.7	38.6	43.2	48.8	38.7					
							Gnaphalium uliginosum					
chisel	oat/pea/vetch	7324	2200	4064	4320	550	2640	†				
chisel	barley	9239	6493	16237	10217	1157	11474					
moldboard	oat/pea/vetch	8286	3578	6016	4684	1446	5989					
moldboard	barley	9211	5353	14072	7110	1119	12388					
			ANOVA (p) on √ (x+1) transformed data						ANOVA (p) on untransformed data			
								Year	0.036	NS	0.016	<0.001
Tillage (T) effect		--§	NS	NS	NS	NS	NS	Year x T	NS	NS	NS	NS
Rotation crop (R) effect		NS	0.033	0.024	0.019	NS	0.003	Year x R	NS	NS	0.016	<0.001
TxR effect		--	NS	NS	NS	NS	NS	Year x T x R	NS	NS	NS	NS
CV_T %		--	26.4	10.9	16.2	24.6	17.1					
$CV_{R \text{ and } TxR}$ %		81.1	27.2	36.0	21.5	43.6	24.2					
							Total Weeds					
chisel	oat/pea/vetch	12444	6988	6493	6270	2024	5802	†				
chisel	barley	13537	10159	18966	12130	2780	14571					
moldboard	oat/pea/vetch	13817	7968	8127	6709	3172	8965					
moldboard	barley	16479	10230	17889	9377	2425	15317					
			ANOVA (p) on √(x+1) transformed data						ANOVA (p) on untransformed data?			
								Year	0.004	0.008	0.004	<0.001
Tillage (T) effect		--§	NS	NS	NS	NS	NS	Year x T	NS	NS	NS	NS
Rotation crop (R) effect		NS	0.004	0.013	0.014	NS	0.002	Year x R	NS	NS	0.016	<0.001
TxR effect		--	NS	NS	NS	NS	NS	Year x T x R	NS	NS	NS	NS
CV_T %		--	28.1	4.6	12.4	17.2	12.9					
$CV_{R \text{ and } TxR}$ %		17.6	7.3	26.6	15.1	20.1	18.3					

† - untransformed means presented.
‡ - NS - nonsignificant at $p > 0.1$.
§ -tillage treatments were initiated in 1993.
¶ mean separation for the year x T x R interaction; different letters indicate significantly different polynomial trends at $\alpha < 0.1$.
# potato growing seasons.

Table 2.6. Weed density in potato years as affected by rotation crop and tillage.

Tillage system	Rotation crop in previous year	Weed number per m^2 1993	1995	1997		year effect polynomial trends linear	quadratic
				Chenonodium album			
chisel	oat/pea/vetch	39.5	3.3	3.3	†		
chisel	barley	45.3	7.8	4.0			
moldboard	oat/pea/vetch	53.0	5.8	3.0			
moldboard	barley	44.3	10.0	5.8			
				ANOVA (p)‡			
					Year	0.002	0.003
Tillage (T) effect		NS§	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		NS	NS	NS	Year x R	NS	NS
TxR effect		NS	NS	NS	Year x T x R	NS	NS
CV_T %		46.0	39.5	37.0			
$CV_{R \text{ and } RxT}$ %		31.4	34.1	16.7			
				Crucifer Complex			
chisel	oat/pea/vetch	17.3	37.8	43.3	†		ab ¶
chisel	barley	2.8	23.0	43.3			a
moldboard	oat/pea/vetch	12.0	11.0	15.0			ab
moldboard	barley	5.3	20.8	14.5			b
				ANOVA (p)‡			
					Year	<0.001	0.001
Tillage (T) effect		NS	0.002	0.003	Year x T	co.05	NS
Rotation crop (R) effect		NS	NS	NS	Year x R	NS	NS
TxR effect		NS	NS	NS	Year x T x R	NS	0.021 §
CV_T %		42.8	8.6	15.7			
$CV_{R \text{ and } RxT}$ %		64.3	38.3	46.9			
				Total Weeds			
chisel	oat/pea/vetch	66.0	43.3	46.8	†		ab¶
chisel	barley	67.3	37.3	53.0			a
moldboard	oat/pea/vetch	74.5	19.3	19.5			ab
moldboard	barley	61.5	32.8	21.3			b
				ANOVA (p)‡			
					Year	NS	<0.001
Tillage (T) effect		NS	0.079	0.006	Year x T	NS	NS
Rotation crop (R) effect		NS	NS	NS	Year x R	NS	NS
TxR effect		NS	NS	NS	Year x T x R	NS	0.016 §
CV_T %		32.8	15.8	15.2			
$CV_{R \text{ and } RxT}$ %		17.9	22.5	23.4			

† - means presented are untransformed.

‡ - ANOVA for individual years was performed on $\sqrt{(x+1)}$ transformed data. Repeated measures ANOVA for polynomial trends over years was performed on untransformed data.

§ - NS - nonsignificant at $p > 0.1$.

¶ - mean separation for the year x T x R interaction; different letters indicate significantly different polynomial trends at $\alpha < 0.1$.

have a significant effect on the germinable seedbank of the 'crucifer complex' (Table 2.5). The germinable soil seedbank of the crucifer complex in 1997 was much higher in chisel than in moldboard-plowed plots. The preceding wet season (1996), favored biomass and seed production of the 'crucifer complex' (Table 2.4), enhancing the difference between seed density near the soil surface (freshly-shed seeds) and deeper in the soil profile prior to the tillage operations. These results support our hypothesis that following high seed production chisel-plowing results in greater weed seed densities near the soil surface and greater weed plant densities than does moldboard-plowing.

Crucifer density and biomass in potato increased more over time in chisel-plowing than in moldboard-plowing (Tables 2.6 and 2.7), supporting the hypothesis that weed species that increase over the course of the study will increase faster in chisel than in moldboard-plowed treatments. The increase in the germinable spring seedbank of the 'crucifer complex' was smaller for moldboard-plowed plots than for chisel-plowed plots (Table 2.5). Whether the difference between the seed densities in the soil seedbank would remain as large over an extended period of time cannot be predicted from this study. If seed mortality at depths to which moldboard-plowing brings the seeds is relatively low, it could be expected that the two tillage treatments would become more similar over time as the entire soil profile in the moldboard-plow treatment becomes filled with more seeds. In addition seeds closer to the soil surface tend to have higher mortality rates than seeds buried deeply (Schlink, 1994; Reeves et al. 198 1; Zhang et al. 1997).

Table 2.7. Weed biomass in potato years as affected by rotation crop and tillage.

Tillage system	Rotation crop in previous year	Weed dry matter [g m^{-2}] 1993	1995	1997		year effect polynomial trends linear	quadratic
					Chenonodium album		
chisel	oat/pea/vetch	1.58	0.38	0.75	†		
chisel	barley	0.63	1.77	3.85			
moldboard	oat/pea/vetch	0.35	3.35	3.35			
moldboard	barley	0.61	0.27	4.93			
					ANOVA (p)‡		
					Year	NS	NS
Tillage (T) effect		NS§	NS	NS	Year x T	NS	NS
Rotation crop (R) effect		NS	NS	NS	Y e a r x R	N S	NS
TxR effect		NS	NS	NS	Y e a r x T x R	N S	NS
CV_T %		94.8	95.8	79.0			
$CV_{R\ and\ RxT}$ %		138.5	148.3	65.0			
					Crucifer Complex		
chisel	oat/pea/vetch	29.0	19.1	83.5	†		
chisel	barley	6.6	3.2	115.9			
moldboard	oat/pea/vetch	22.3	13.9	47.4			
moldboard	barley	14.9	9.4	45.7			
					ANOVA (p)‡		
					Year	< 0.001	0.003
Tillage (T) effect		NS	NS	NS	Year x T	0.100	0.100
Rotation crop (R) effect		NS	NS	NS	Year x R	NS	NS
TxR effect		NS	NS	NS	Y e a r x T x R	N S	NS
CV_T %		48.3	32.0	29.8			
$CV_{R\ and\ RxT}$ %		97.3	42.8	22.7			
					Total Weeds		
chisel	oat/pea/vetch	31.0	19.7	84.3	†		
chisel	barley	11.3	8.9	126.1			
moldboard	oat/pea/vetch	22.8	18 6	51.3			
moldboard	barley	21.2	11.1	50.6			
					ANOVA (p)‡		
					Year	< 0.001	0.004
Tillage (T) effect		NS	NS	NS	Year x T	0.100	0.100
Rotation crop (R) effect		NS	NS	NS	YearxR	<0.1	NS
TxR effect		NS	' NS	NS	Year x T x R	<0.1	NS
CV_T %		36.1	11.2	20.4			
c $v_{R\ and\ RxT}$ %		78.0	22.6	15.8			

† - means presented are untransformed.

‡ - ANOVA for individual years was performed on $\sqrt{(x+1)}$ transformed data. Repeated measures ANOVA for polynomial trends over years was performed on untransformed data.

§ - NS - nonsignificant at $p > 0.1$.

Higher rates of fatal germination, seed predation and exposure to a harsher physical environment closer to the soil surface result in this gradient of seed mortality over burial depth.

Liebman et al. (1996) detected significant tillage effects on the soil seedbank and weed density in potato after the first tillage event took place in their study. The initially dominant weed species, C. album., had lower densities of seeds in the soil following moldboard than following chisel-plowing, and the total weed density in the potato crop was higher in chisel than in moldboard-plowed plots. This early detection of a tillage effect was a consequence of much higher weed biomass production (164 g m^{-2}) and resulting weed seed production in the rotation crop phase than was observed in the present study. Almost the entire weed biomass in the first year of the study by Liebman et al. (1996) consisted of C. album.

Weed Community Composition

In 1992 and 1994, weed species richness was significantly greater in barley than in oat-pea-vetch (Table 2.8), and this rotation crop effect carried through into the potato phase in 1995. In all other years, no significant difference was detected. This finding is consistent with the hypothesis that weed species richness is lower in crops with greater weed suppressive ability. In terms of weed management, reduced weed species richness can be considered positive, because fewer species present in a field form a smaller pool of weed species that might become dominant and difficult to control (Clements et al., 1994).

Table 2.8. Weed species richness and evenness of plants growing in the field.
Species richness (S = number of species present) and evenness of weeds (E = $(-\Sigma p_i \ln pi) / \ln S$, p_i = proportion of sample belonging to sample i).

Tillage system	Rotation crop	1992	1993¶	1994		1995¶	1996	1997¶
				Weed species richness				
chisel	oat/pea/vetch	3.3	5.3	2.3	d†	2.3	8.8	2.5
chisel	barley	6.8	6.8	8.0	a	3.5	8.3	4.0
moldboard	oat/peaJvetch	3.3	6.8	4.0	c	2.5	6.5	3.0
moldboard	barley	6.8	6.8	6.5	b	3.5	9.5	3.0
				ANOVA (p)				
Tillage (T) effect		--‡	NS§	NS		NS	NS	NS
Rotation crop (R) effect		<0.001	NS	<0.001		0.003	NS	NS
TxR effect		--	NS	0.001		NS	NS	NS
CV_T %		--	28.3	19.1		29.1	24.2	27.7
$CV_{R \text{ and } RxT}$ %		25.6	19.7	10.8		16.3	24.0	27.7
				Weed species evenness				
chisel	oat/pea/vetch	0.66	0.60	0.56		0.47	0.69	0.58
chisel	barley	0.33	0.69	0.75		0..64	0.64	0.68
moldboard	oat/pea/vetch	0.66	0.47	0.71		0.58	0.68	0.61
moldboard	barley	0.33	0.53	0.76		0.78	0.69	0.68
				ANOVA (P)				
Tillage (T) effect		--‡	NS	NS		NS	NS	NS
Rotation crop (R) effect		0.002	NS	NS		0.040	NS	NS
TxR effect		--	NS	NS		NS	NS	NS
CV_T %		--	39.8	33.4		25.5	18.4	31.6
$CV_{R \text{ and } RxT}$ %		32.2	30.1	34.3		22.8	9.2	32.2

† mean separation for T x R, different letters indicate significant differences Tukey's multiple comparison test at $p < 0.05$.
‡ tillage treatments were initiated in 1993.
§ NS - nonsignificant at $p > 0.1$.
¶ potato growing seasons

Weed species evenness in oat-pea-vetch compared to barley was greater only in the first year of the study, 1992 (Table 2.8). Thus, the hypothesis that more weed suppressive crops result in greater evenness in weed community composition than do less weed suppressive crops is supported by the data for this one year only. In 1995, a dry year, weed species evenness was significantly greater following barley than following oat-pea-vetch (Table 2.8). Because 1995 was the potato phase of the experiment this result can not be used directly to reject the hypothesis, however, because weed density in the current year tends to be correlated with weed density and seed production in the previous season (Liebman et al., 1996) this result can be used as an indication that the hypothesis might not hold under all conditions. In all other years, there was no significant difference in weed species evenness between the two rotation crops. The lack of a consistent significant difference between the two rotation crops could be due to oat-pea-vetch not consistently suppressing the weeds of the 'crucifer complex' more than barley. Greater evenness is desirable from an agricultural point of view, because it indicates that no one weed species is dominant (Clements et al., 1994).

Shifts in Weed Community Composition

Overall, the density of C. album in the germinable seedbank declined over the course of the experiment, whereas the seedbank of the 'crucifer complex' increased (Table 2.5). Plant density and biomass of C. album in rotation crop years remained within the same range throughout the duration of the experiment (Table 2.2 and 2.4), but germinable seeds in the seedbank declined to about a quarter of the original density over

the same time period (Table 2.5). Thus, density of germinable C. album seeds in the soil did not appear to be the limiting factor for C. album establishment and biomass production in rotation crop years. However, in potato, C. album density declined over the period of the study as did the soil seedbank (Table 2.5 and 2.6). The decline of C. album density in potato was even steeper than the decline in the seedbank. This probably resulted in part from the reduced seedbank in later potato years. In addition, cultivations in 1993 were done using finger-weeders over the rows and S-tines between the rows and took place later in the growing season than in 1995 and 1997, when spring-tine cultivations were used. The earlier cultivations in 1995 and 1997 probably resulted in higher weed mortality rates as weed seedlings generally are much more sensitive to cultivation when they are smaller than when they are larger (Rasmussen, 1990). Differences in efficacy and selectivity of a cultivation can be greater due to timing and driving speed than the type of implement used (Rasmussen, 1992).

C. album biomass in the potato years increased slightly with time in spite of the opposite trend in its seedbank and density (Tables 2.5, 2.6, and 2.7). In 1997, the increased biomass of C. album can be explained by reduced potato competitive ability due to poor seed piece quality. In 1995, the increase in C. album biomass possibly resulted from an indirect effect of the drought. The vigor of potato was reduced compared to normal years, reducing its ability to compete with C. album.

Infestation by the 'crucifer complex' increased over the period of the study in all parameters measured (Tables 2.2, 2.4 , 2.5, 2.6 and 2.7). In both tillage systems, there was a marked increase in 'crucifer complex' biomass in 1997 compared to earlier years. This was probably the consequence of (i) a high germinable seedbank in the spring of 1997

following high crucifer complex biomass production in the wet conditions of 1996, and (ii) reduced competition from the potato crop due to poor seed piece quality. In rotation crop years there were no significant differences in density and biomass trends of the crucifer complex between the two tillage practices.

The pattern of a population increase for the 'crucifer complex' concurrent with a population decrease for C. album is similar to the results of a study by Liebman et al. (1996). They found a decrease in C. album biomass over the course of their four-year study of oat-potato and berseem clover-potato rotations, and attributed it to interference from the crucifer species with supporting evidence in their path analysis. The data from our study, however, contain no statistically significant relationship that would support the hypothesis of interference between these weed species. The treatments generally influenced the populations of the crucifer complex and C. album in the same direction. If any negative interactions between the weed species occurred, they were less pronounced than the treatment effects and consequently not detectable. An alternative hypothesis to explain the trends observed is that the management practices used were more favorable to the 'crucifer complex' and more disadvantageous to C. album. This appears likely, because the crucifer species exhibited very rapid early growth and development and consequently suffered less from competition with the rotation crops, particularly oat-pea-vetch. Crucifer seeds are larger than C. album seeds, resulting in larger seedlings early in the growing season. The optimum depth of emergence of the crucifer species also tends to be greater (l-3 cm) than that of C. album seeds (0 cm) (Chapter 3). Consequently, it is possible that spring-tine harrowing may differentially kill more C. album than crucifer seedlings.

In the initial seedbank, the crucifer complex was at a relatively low density, whereas C. album was at a high density (Table 2.5). The density of germinable seeds of the crucifer complex in the soil increased over time, whereas the density of C. album seeds decreased. If weather conditions and crop management practices before the onset of the study were similar to the conditions during the study, the expectation for the initial seedbank would be that crucifer seeds were relatively more numerous and C. album less numerous. Why did the initial seedbank differ from this expectation? One possible explanation is that at the study site some years of high weed seed production by both the 'crucifer complex' and C. album were followed by a number of years with quite successful weed control resulting in very low weed seed production prior to the onset of this study. Both the seeds of the 'crucifer complex' and C. album can survive for a long time in the soil. However, the seeds of the 'crucifer complex' have a high rate of germination and thus experience a high loss from the seedbank in the first year after seed shed (53-60 %, Kolk, 1962; 47.5 - 82%, S. Ullrich, unpublished data, 1994-1997), whereas a large proportion of C. album seeds are dormant in the first spring after seed shed resulting only in a small loss to germination (6 - 8 %, Kolk, 1962; 0.3 - 14.9 %, S. Ulhich, unpublished data, 1996-1997). Consequently, a few years of low weed seed production could shift the ratio of the weed species composition in the soil seedbank in favor of C. album.

Weed Infestation in Potato and Its Effects on Potato Yield

Total weed density in potato years decreased over the period of the study with mean values of 67, 33 and 35 m^{-2} for 1993, 1995 and 1997, respectively (Table 2.6). This decrease was primarily due to a decrease in the density of C. album (Table 2.6). In contrast, total weed biomass in potato years was much higher in 1997 (78.1 g m^{-2}) than in 1993 (21.6 g m^{-2}) and 1995 (14.6 g m^{-2}). This increase in total weed biomass was due to an increase in the biomass of the crucifer complex (Table 2.7).

Two factors may have contributed to the low total weed biomass observed in 1995 (Table 2.7): (i) a warm and dry season (Table 2.3), and (ii) the use of a spring-tine harrow before potato emergence. The high weed biomass in 1997 was probably due to poor potato seed quality, resulting in many skips in the potato rows and reduced competition with weeds.

US #1 and total tuber yields followed similar patterns in all years (Table 2.9), and consequently only US # 1 yields will be discussed. Mean US #1 yield in 1993 was 35.3 Mg ha“, which was comparable to average commercial yields for northern Maine (NASS, 1997). In 1995, yields in this study (mean = 18.0 Mg US #1 ha-‘) and on commercial potato farms in northern Maine were low due to the dry season. Yields in the experiment in 1997 were low (19.1 Mg US #1 ha^{-1}) due in part to planting of low quality seed pieces.

There was a 27.8% reduction ($p < 0.001$) of US #1 tuber yield due to weeds in 1997 (Table 2.9). In 1993 and 1995, potato yield reduction due to weeds was not significant ($p > 0.05$). The significant potato yield loss in 1997 occurred at the same time as a substantial increase in the biomass of the crucifer complex (Table 2.6 and 2.7). Thus,

Table 2.9. Potato yield as affected by rotation crop, tillage and weeds.

Tillage system	Rotation crop in previous vear	Supplemental weed control	Tuber yield [Mg ha^{-1}]†					
			1993		1995		1997	
			US#1	Total	US#1	Total	US#1	Total
chisel	oat/pea/vetch	yes	36.1	42.6	18.9	20.9	25.4	27.7
chisel	oat/pea/vetch	no	32.1	39.0	16.0	19.0	14.5	15.8
chisel	barley	yes	36.3	43.0	14.2	18.4	20.9	23.0
chisel	barley	no	33.1	39.4	16.3	19.7	15.2	16.9
moldboard	oat/pea/vetch	yes	34.5	40.8	21.2	24.4	19.3	21.2
moldboard	oat/pea/vetch	no	35.0	41.2	14.5	18.2	16.5	18.5
moldboard	barley	yes	39.1	45.4	21.6	246	23.2	25.1
moldboard	barley	no	36.0	41.7	21.5	25.5	18.0	20.2
						ANOVA (p)†		
Tillage (T) effect			NS‡	NS	0.044	0.051	NS	NS
Rotation crop (R) effect			NS	NS	NS	NS	NS	NS
Weed infestation (W) effect			0.086	NS	NS	NS	0.001	0.001
TxR effect			NS	NS	NS	NS	NS	NS
TxW effect			NS	NS	NS	NS	NS	NS
RxW effect			NS	NS	NS	NS	NS	NS
TxRxW effect			NS	NS	NS	NS	NS	NS
CV_T %			11.3	11.2	14.8	14.0	24.7	24.3
$CV_{R,\ W,\ and\ interactions}$ %			10.7	9.8	28.3	21.6	23.8	20.7

† untransformed means presented, ANOVA performed on untransformed data.
‡ - NS - nonsignificant at $p > 0.1$.

it appears likely that some of the potato yield reduction resulted from increasing interference by the 'crucifer complex'. The extent of this yield reduction, however, was most likely exacerbated by poor potato seed piece quality resulting in many skips and reduced potato vigor and competitive ability in 1997. The hypothesis that potato yield reduction due to weeds is greater at higher weed density and biomass is thus only supported partially by the results of this study. Greater yield reduction due to an increase in total weed biomass is supported by the data, but no relationship between total weed density and yield loss was detected.

Liebman et al. (1996) found a consistent potato yield reduction due to weeds in an experiment in which oat or berseem clover were grown in alternate years with potato. Mean total weed biomass in that study was 63 g m^{-2} in 1991 and 86 g m^{-2} in 1993, which was much higher than in the present study in 1993 and 1995. Total weed plant density was also much higher in their study, with 208 m^{-2} present in 1993. Liebman et al. (1996) reported that in one of two years, the difference in weed infestation between moldboard- and chisel-plowed treatments was sufficient to result in significantly smaller potato yields in chisel- than in moldboard-plowed plots. The present study led to an unexpected additional result: in the dry 1995 season, US # 1 yields in chisel-plowed plots were 17% ($p = 0.044$) lower than yields in moldboard-plowed plots (Table 2.9). Even though chisel-plowed plots had a significantly higher 'crucifer complex' density and a trend towards higher total weed density, this yield reduction was most likely not the sole result of the weed infestation, because the yield difference occurred in weed-free plots as well. The difference in yield may be due to reduced bulk density and soil firmness resulting in increased rooting volume and reduced water stress following moldboard compared to

chisel-plowing (Grant and Epstein, 1973; Halderson et al., 1993). A number of studies reported improved potato yields with reduced soil density (Bishop and Grimes, 1978; Grimes and Bishop, 197 1; Ibrahim and Miller, 1989).

Economic Considerations

To be adopted by farmers, weed management systems must be economically viable. The green-manure mixture of oat, pea and hairy vetch is more weed-suppressive than barley, but there is no direct revenue from it. In addition, seed costs, especially pea, are high, if the seed is purchased commercially ($319.31 ha-' in 1994, E. Mallory, unpublished data, 1995). Based on current prices for herbicides, fertilizers, field operations, barley seed, and barley revenue (E. Mallory, unpublished data from a dealer survey, 1995) and an assumption of a 75 kg ha^{-1} N-replacement value for potatoes grown after legume green-manure (Porter and Sisson, 1991), the seed for the green-manure mixture would need to be available to growers at $0.31 ha^{-1} to achieve the same returns as with a conventional system using barley as the rotation crop, herbicides, and synthetic fertilizers.

The crop management system of potatoes in rotation with barley as used in this study, i.e. with one cultivation with a spring-tine harrow in potato ($3.90 ha-', E. Mallory, unpublished data, 1996), has lower costs than the conventional system using herbicides ($76.52 ha", E. Mallory unpublished data, 1996). In order to break even with the conventional system, potato yield loss due to weeds should not be greater than 1.7% (assuming average Maine potato yield of 30.8 Mg ha-' for 1996 (NASS, 1997) and a price

of \$139 Mg^{-1}, unpublished data, E. Mallory, 1994). Each additional spring-tine cultivation in the rotation would need to reduce potato yield loss by a minimum of 0.091% to recover the cost of the cultivation, assuming no negative effects of the cultivation on the crop.

Planting a forage crop could improve the revenue from a weed-suppressive crop in rotation with potatoes. This would introduce mowing as an additional practice to reduce weed reproduction. Seed production of spring-germinating weeds might be decreased by leaving the forage crop in the field for a second season. A. Files and S. Smith (unpublished data, 1999) studied the economics of a five-year potato rotation (potato-potato-barley undersown with alfalfa-alfalfa-alfalfa) in northern Maine and found the mean annual revenue of this rotation was similar to a two-year, potato-barley rotation. Weed suppressive effects of alfalfa have been reported repeatedly, most recently by Clay and Aguilar (1998) who reported very low weed biomass in alfalfa in the year following establishment and reduced weed seedbanks in corn following alfalfa.

Future research should concentrate on identifying rotation crops that can suppress the species of the 'crucifer complex' either competitively or by breaking their life-cycle. Preferably these should be crops that result in revenue. Such crops could be (i) forage crops left in the field for two consecutive seasons or planted in the fall, or (ii) fast-growing, warm-season crops that can be harvested as forage.

3. MODEL OF CRUCIFEROUS WEED POPULATION DYNAMICS IN POTATO-BASED CROP ROTATIONS I: MODEL STRUCTURE, VALIDATION AND LONG-TERM SIMULATIONS

Abstract

A simulation model of the population dynamics of a complex of cruciferous weed species (Brassica rapa (birdsrape mustard), Brassica kaber (wild mustard), and Ranhanus raphanistrum (wild radish)) in two-year potato rotations with contrasting primary tillage practices (moldboard- vs. chisel-plow) and contrasting crops in rotation with potato (barley, grown for grain and oat-pea-vetch, grown as green-manure) was developed and validated. The model incorporates detail in the depth structure of the seedbank, seedling emergence, and size-dependent seedling mortality due to spring-tine harrowing and hilling. Weather was included in the model by categorizing growing seasons according to their precipitation levels. Including density-dependent functions in addition to weather, resulted in simulation results closer to field observations. In 20-year simulations no consistent long-term differences between tillage and rotation crop treatments occurred; variation due to weather was greater than differences between treatments. The seedbank increased over the simulation period.

Introduction

Many farmers and researchers have been searching for alternatives to heavy reliance on herbicides for weed management in recent years. The amount of herbicides applied to farmers' fields annually is higher than the combined amount of insecticides and fungicides (Aspelin, 1994) resulting in a large expense for farmers. In addition, with increasing frequency, herbicides do not result in adequate weed control, since herbicide-resistant weeds may evolve (Heap, 2000). The heavy use of herbicides has increased environmental concerns, as reports of herbicides contaminating sources of drinking water become more numerous (Hallberg, 1989, Thurman et al., 1991).

Ninety-eight percent of the area planted with potato in Maine and 87% of the area planted with potato in the USA were treated with herbicides in 1997 (ERS, 1997). In potato cropping systems in northern Maine, Brassica rapa L. subsp. sylvestris (1.) Janchen (birdsrape mustard) became a dominant weed species after the use of herbicides was discontinued (Liebman et al., 1996). A field study reported in Chapter 2 suggested that increasing populations of this and two closely related cruciferous weed species (Raphanus raphanistrum L. (wild radish) and Brassica kaber (D.C.) L.C. Wheeler var. pinnatifida (Stokes) L.C. Wheeler (wild mustard) resulted in increased potato yield loss. These three species cannot be distinguished in the seedling stage and have a fairly similar ecology. In this paper these three species will be referred to as the "crucifer complex". In order to devise effective management practices to reduce the populations of the 'crucifer complex' it is important to increase the understanding of the life-cycle of these weeds and how the different stages in the life-cycle respond to different management practices. This can be achieved by constructing a population dynamics simulation model. Such a

model can be used to identify areas in which more research is needed and which stages in their life-cycle these weeds respond particularly sensitive to changes in parameters. Management practices acting on those stages would be particularly effective in controlling the populations. The research that we report on in this paper involved the construction of a computer simulation model of the population dynamics of this 'crucifer complex' in potato rotations in northern Maine.

A number of models have been developed to simulate the long-term dynamics of annual weed populations in cereal cropping systems (Cousens et al. 1986; Debaeke, 1988; Debaeke and Sebillote, 1988; Doyle et al. 1986; Firbank and Watkinson, 1986; Gonzalez-Andujar and Femandez-Quintanilla, 199 1; Kaul, 1992; Watkinson et al., 1989; Zwerger and Hurle, 1988). Jordan et al. (1995) and Lindquist et al. (1995) modeled weed population dynamics in corn-soybean cropping systems. For modeling purposes weed populations are often divided into four stages: seedbank, seedlings, mature weeds, and newly shed seeds (e.g. Lindquist et al., 1995; Zwerger and Hurle, 1988; Röttele, 1980; Kaul, 1992). Various elaborations on this structure have been used depending on the objective of the model and the biology of the weed and the cropping system (Cousens, et al., 1986; Gonzalez-Andujar, 1997; Gonzalez-Andujar and Femandez-Quintanilla, 199 1; Jordan et al., 1995).

Most weed population dynamics models to date only include herbicides as weed control methods. Mechanical weed control has been included in only a few models. Jordan et al. (1995) incorporated mechanical weed control into their model, but not as a separate component of each specific crop management practice. Jordan (1993) included lower weed survival rates in furrows than in ridges to simulate cultivation. No published

purely demographic model to date includes actual mortality rates due to the type of cultivation and timing of cultivation. Only the model "WEPOM" (Danuso and Zanin, 1989) contains specific weed survival rates dependent on weed seedling stage, timing and the type of cultivation, however, "WEPOM" integrates mechanistic, physiologically based crop-weed interactions within a weed population dynamics model.

Van der Weide and Van Groenendael (1990) analyzed the complexity necessary to construct a demographic model of Galium aparine (L.) (cleavers) for optimization of the timing of management practices and to compare weed population responses among different cropping systems. They concluded that for predictive purposes, parameters that vary strongly with abiotic environmental factors need to be modeled based on physiological principles. An example for such a model is "WEPOM" (Danuso and Zanin, 1989) in which mechanistic crop-weed interactions are integrated within a weed population dynamics model resulting in a very flexible model that can be applied to many situations and includes environmental variability, however, it requires a large number of parameters to be estimated. Modeling at the level of physiological processes is much more data intensive than demographic modeling. Colbach and Debaeke (1998) suggest using parameters that integrate crop and environmental factors. They suggest estimating these parameters from simulations with mechanistic weed-crop models. In a review of weed population dynamics models, Colbach and Debaeke (1998) suggested a number of factors that should be included in future weed population dynamics models. Some of the factors are included in our model: detailed simulation of seedbank and seedling emergence over depth, weather, seed production dependent on crop, weed density,

inclusion of mechanical weed control methods and inclusion of the option of no herbicides.

The model we developed is a population-projection model (van Groenendael et al., 1988; Caswell, 1989) similar in general structure to the model constructed by Jordan et al. (1995) but with a number of important differences. Our model has more detail in weed seed distribution over soil depth, depth dependent emergence, and seed survival. We also include a relatively detailed simulation of the population biology of the species of the crucifer complex, as well as simulations of a number of crop management practices and mechanical weed control. In the field studies performed in order to estimate parameters for this model it was observed that weather strongly affects these estimates. We decided to include broad categories of weather patterns in this model to account for the weather dependent annual differences in the behavior of the weed population.

The objectives of this study were to develop a model that simulates the population dynamics of a complex of crucifer species in two year potato rotations and then use this model to compare the long-term effect of two contrasting crops in rotation with potato and two contrasting primary tillage practices.

Materials and Methods

Model Structure

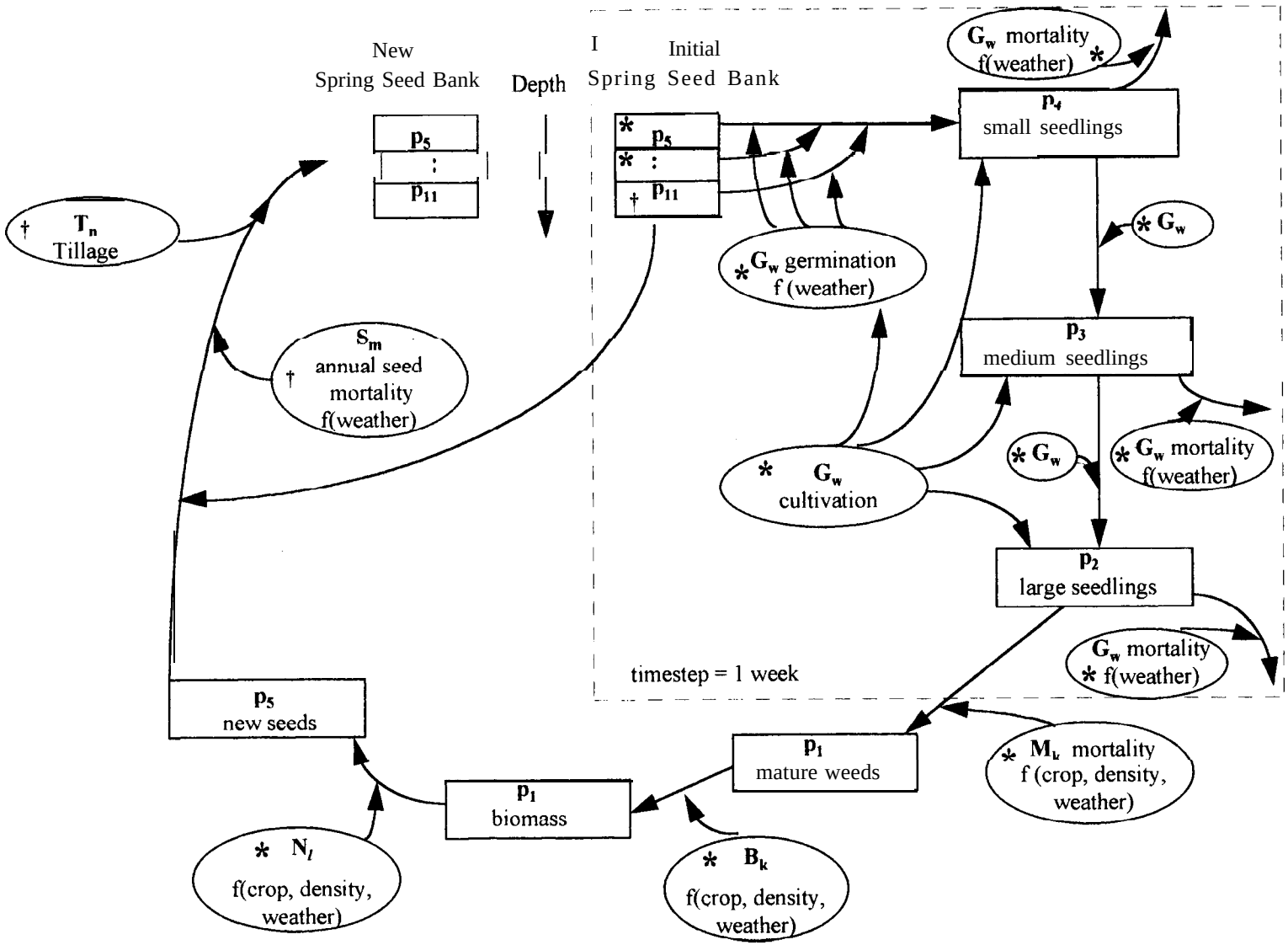
Our model is a difference equation model programmed in the computational environment MATLAB® 4 (The Math Works Inc., 1995). It consists of a population

vector that is adjusted by multiplying this vector with a series of transition matrices throughout the time course of the simulation (see Appendix A).

The weed population of the crucifer complex addressed in this model is partitioned into seven depth intervals to represent seed density in the soil seedbank, because the species of interest have a relatively long seed longevity in the soil (Barralis et al., 1988). Due to their relatively small size, germination and successful emergence are strongly influenced by the depth of seed burial (Barralis, et al., 1988; Grundy et al., 1996). A number of studies also show that weed seed survival in the soil is influenced by depth of burial (Froud-Williams et al. 1984; Kolk, 1962). Three size classes of seedlings represent the age structure of the pre-flowering crucifer population. The number of mature reproducing weeds and their biomass are tracked by the model and represent the final age class in the crucifer population (p_1; Fig. 3.1). Age differences between seeds in the seedbank were not taken into account in the model.

The model does not have a time step of consistent length throughout the year. The first four weeks after planting in rotation crops and the first five weeks in potato have a time step of one week. During these initial weeks the pattern of crucifer emergence over time is important in determining the appropriate survival rates. Smaller, younger seedlings tend to have lower chances of survival during cultivations and natural mortality factors are more likely to kill small weeds. They also suffer more stress due to competition from neighboring larger plants. Once the crops are too large for cultivation and newly emerging weeds will tend to remain small due to shading by the crop canopy, the model uses time steps for events that occur once every season. Seedlings that survive the cultivations are subject to some natural mortality before reaching final density at

Figure 3.1. Schematic diagram of the simulation model.
$p_{1...11}$ = population vector, G_w = transition matrices with parameters for germination and seedling survival, * - parameters derived from field experiments described here, † - parameters derived from the literature. For more detailed descriptions of other model components refer to the text. encompasses the part of the model that has a timestep of 1 week, ▭ - state variables, 0 - conversion factors.


New
Spring Seed Bank
Depth
I Initial
Spring Seed Bank
p5
p11
† Tn
Tillage
Sm
† annual seed
mortality
f(weather)
* Gw germination
f (weather)
Gw mortality
f(weather) *
p4
small seedlings
* Gw
p3
medium seedlings
* Gw
* Gw mortality
f(weather)
* Gw
cultivation
p2
large seedlings
Gw mortality
* f(weather)
timestep = 1 week
p5
new seeds
p1
mature weeds
* Mk mortality
f (crop, density,
weather)
p1
biomass
* Nl
f(crop, density,
weather)
* Bk
f(crop, density,
weather)

maturity (as would be measured in the field in the first half of August). In potato years the weed mortality is modeled as a density-independent process. Mortality of seedlings in potato is assumed to be dominated by the mortality due to cultivation and thereby, reducing the density to levels too low to result in significant density-dependent mortality. In rotation crops the weed seedling survival to maturity is modeled as a density-dependent hyperbolic function (Cousens, 1986; Doyle, 1991). The density of mature weeds is then converted to crucifer biomass as a density-dependent function occurring only once every season. When the seeds on these mature weeds are predicted to ripen the biomass is converted to a number of seeds ($p_1 \rightarrow p_5$; Fig. 3.1). These seeds fall onto the soil surface in late summer or early fall. They are added to the soil seedbank in the depth-interval from O-l cm (p_5; Fig. 3.1). Annual mortality of seeds from the soil seedbank is modeled once every year following seed production ($S_,$; Fig. 3.1). Primary tillage and seedbed preparation are modeled as happening in the spring, prior to planting, but after annual seed mortality has occurred. Primary tillage occurs only every second year prior to planting of potato. Redistribution of the weed seedbank is modeled concurrently (in the same transition matrix) for primary tillage and seedbed preparation using a disk and a spring-tooth harrow ($T_,$; Fig. 3.1). Seedbed preparation is assumed to mix the soil evenly and distribute the seeds evenly over the entire top six centimeters of the soil. In rotation crop years no primary tillage, just seedbed preparation with a field cultivator occurs. It is assumed that no soil disturbance occurs below six centimeter depth. Seed movement due to spring-tine harrowing and hilling is not modeled.

The first element in the population vector every season represents the number of mature weeds and is converted to crucifer biomass at the time when all but very late-

emerging cruciferous weeds reach maturity (about 11 weeks after planting). Very late emerging cruciferous weeds are ignored in the model as a constituent of the above-ground weed population. They emerge so much later than the crops that it is assumed that they would be shaded and therefore contribute an insignificant amount to the overall crucifer biomass and wouldn't contribute to seed production. However, they are incorporated into the parameters estimated for the loss of seeds from the soil seedbank. Seed immigration and emigration is assumed to be of minimal importance and is not included in the model.

Difference Equations

A detailed description of the population vector (p(t)) and the transition matrices used in the difference equations can be found in Appendix A.

The parameters for germination, mortality and growth from one seedling class to the next used in the model apply to a time step of w = 1 week. During germination and weed seedling growth and early weed seedling mortality due to natural causes and cultivations the weed population vector is updated by the germination, seedling survival and development transition matrix $\mathbf{G}_w$:

$$\mathbf{p}(w+1) = \mathbf{p}(w)\,\mathbf{G}_w \qquad (1)$$

w = week

For all the following equations each of the transitions happens once in a year, i.e., the time-step is one year. The transitions follow each other in the order in which the equations are arranged.

Survival of weed seedlings to mature weeds (density-dependent in rotation crops):

$$\mathbf{p}(k+1) = \mathbf{p}(k)\,\mathbf{M}_k \qquad (2)$$

$\mathbf{M}_k$ = transition matrix for survival to mature weeds,

k = once a year about 11 weeks after planting

Biomass of mature weeds (density-dependent):

$$\mathbf{p}(k+1) = \mathbf{p}(k)\,\mathbf{B}_k \qquad (3)$$

$\mathbf{B}_k$ = transition matrix for conversion from weed density to biomass

Seed production (density-dependent in rotation crops):

$$\mathbf{p}(l+1) = \mathbf{p}(l)\,\mathbf{N}_l \qquad (4)$$

$\mathbf{N}_l$ = transition matrix from biomass to number of seeds produced,

I - once a year at the end of each growing season

Seed survival in the soil:

$$\mathbf{p}(m+1) = \mathbf{p}(m)\,\mathbf{S}_m \qquad (5)$$

$\mathbf{S}_m$ = survival matrix for seeds in and on the soil,

m = once a year in the spring before tillage

Redistribution of seeds by tillage and seedbed preparation:

$$\mathbf{p}(n+1) = \mathbf{p}(n)\,\mathbf{T}_n \qquad (6)$$

$\mathbf{T}_n$ = transition matrix for vertical seed movement during tillage and seedbed preparation,

n = once a year in spring before planting

Annual development of the weed population was calculated by combining all the previous equations as a product:

$$\mathbf{p}(t+1) = \mathbf{T}_n\,\mathbf{S}_m\,\mathbf{N}_l\,\mathbf{B}_k\,\mathbf{M}_k\,\mathbf{G}_{wi}\,\mathbf{G}_{wi-1} \ldots \mathbf{G}_{w1}\,p(t) \qquad (7)$$

Sources for Parameter Estimates

All the field derived parameters used in this model were based on the complex of crucifer species rather than one individual species, except for depth of burial effects on emergence over depth. Few data for the species modeled were available in the published literature. Most parameters were therefore obtained from field studies performed at the Maine Agricultural and Forest Experiment Station's Aroostook Farm in Presque Isle, Maine between 1993 and 1997. All studies not published elsewhere are briefly described below.

Seed distribution over depth for initial seedbank

A study described by Liebman et al. (1996) was continued in 1995. The seedbank in four replicate field plots in a potato-oat two-year rotation with moldboard-plowing as

primary tillage practice was sampled in 1995, immediately following plowing and seedbed preparation using a disk and a spring-tooth harrow. Samples from O-5 and 5-10 cm depth were obtained using a bulk density probe with an outer cylinder containing inner rings that could be separated at 5 cm depth. Thirteen samples per plot were drawn with this probe of 5.4 cm diameter, i.e. a total surface area of 297.7 cm^2. The depth interval from 1 O-l 5 cm depth was sampled using a soil probe of 1.9 cm diameter, discarding the part of the sample originating from above 10 cm depth. One-hundred samples per plot were taken with this probe, resulting in 283.5 cm^2 sample surface area per plot. The germinable spring seedbank in these samples was determined by germinating the seeds in a greenhouse as described in Chapter 2. To obtain the seed densities for the depth intervals needed for the model, the depth intervals measured in this field study were divided to create new depth intervals of O-l, 1-2, 2-4, 4-6, and 6-10 cm depth. It was assumed that the seeds were distributed evenly over depth within each measured interval. The seed densities obtained in this way were then converted to percent of the seed density from O-10 cm depth which was used for validation of the model.

The weed seedbank from 15-20 cm depth was not sampled in this study as the soil was extremely rocky and it was not feasible to obtain samples to a depth of 20 cm without pushing rocks into the ground. Instead, a mean value of the seedbank from 15-20 cm depth as percent of the seedbank from 0- 10 cm depth was calculated from Knab and Hurle (1986) for moldboard-plowing averaged over one, two and three passes with a moldboard-plow to account for seeds incorporated in different years.

Effects of depth of burial on seedling emergence

A field experiment designed to estimate seedling emergence from different soil depths was set up on Aroostook Farm in Presque Isle, Maine in 1996 and in 1997 on Roger's Farm in Stillwater, Maine. Twenty-eight cm long pieces of 10 cm diameter PVC pipe were buried in the field vertically leaving a rim of 5 cm above the soil surface. These pipes were filled with soil free of seeds of the crucifer complex, originating from the same forested area on Aroostook Farm, Presque Isle, Maine for both years of the study. Fifty seeds of B. rapa were placed into this soil at specific depths, they were moistened and then left at the soil surface for at least 10 minutes prior to covering them with soil. The seeds were buried at 0, 1, 2, 3, 5, 7.5, 10 and 15 cm depth. In both years a randomized complete block design with 4 blocks was used. Emerging B. rapa seedlings were counted and removed twice a week. The seed used was harvested from fields on Aroostook Farm, Presque Isle, air dried, threshed, cleaned, and stored dry at room temperature. The seed used in 1996 was harvested in 1994 and germinated under optimal conditions in the greenhouse (8 1.6%). The seed used in 1997 was harvested in 1996 and had a higher germination rate of 95.6%. The lower germination rate of seeds harvested in 1994 compared to 1996 could be due to seed age (Barralis et al., 1988), as well as the environmental conditions under which the seeds ripened (Donald, 1993). The seeds produced in 1994 ripened during a dry period, whereas the seeds produced in 1996 ripened during a wet season. Means and standard deviations of the emergence data were determined for each depth and year.

Survival in rotation crops

The survival rates of weeds in three crops, oat and barley grown for grain and a mixture of oat, field pea and hairy vetch grown as a green-manure were determined in a field experiment in 1995 (May through August 40% less precipitation and 1.6°C warmer than 30-year average) and 1996 (May through July 22% more precipitation and 0.5°C colder than 30-year average). The design used, was a randomized complete block design with four blocks, each plot was 4.6 by 7.6 m (Chapter 2).

Four permanent quadrats of 0.25 m^2 size per plot were marked before the crop emerged. The weeds in these quadrats were counted repeatedly over the season. The last count was done by cutting the entire biomass (crop and weeds) in the quadrates, sorting, counting, drying and weighing the weeds by species. In 1995 the weeds were counted 4 times during the season, in 1996 they were counted 3 times.

Survival rates were calculated by subtracting the weed density at the end of the season from the density after complete emergence. This difference was then divided by the density after complete emergence to give the mortality rate. One minus the mortality rate is the survival rate. Density-dependent survival rates were determined using the nonlinear model feature of SYSTAT Version 7.0 (SPSS, 1997). The data were fitted to a hyperbolic model (Cousens, 1986):

$$y = a / (1 + c * x) \qquad (8)$$

y = survival rate, x = density,

a = parameter for maximum biomass per plant,

c = parameter for density-dependence of biomass per plant

This model approaches zero asymptotically, thus never becoming zero or negative with positive parameters. Nonlinear regression was used to estimate parameters of the hyperbolic model from the field data. We used these parameter estimates even if they were not significantly different from zero at $\alpha = 0.05$, because we assumed density-dependent survival of weeds. This assumption was supported by the observation that model runs without inclusion of density-dependence resulted in significant departure from densities observed under field conditions (see results).

Survival in potato

Weed survival in potato under exposure to spring-tine harrowing with a Lely®-weeder and hilling was studied in field experiments at Aroostook Farm in Presque Isle in 1995 and 1996. The experiment in 1995 had two treatments: no versus one preemergence spring-tine cultivation. In 1996 there was an additional treatment with two spring-tine cultivations, one pre- and one postemergence. The experimental design used in both years was a randomized complete block design with four blocks. The plots were 4.6 m (5 rows) wide and 30.5 m long. The experiment was planted with the cultivar 'Katahdin'. In 1995, at 14 days after planting (DAP) the soil had a hard dry crust that was only partially broken up by spring-tine cultivation (at 12 km h^{-1}); in 1996 the first spring-tine cultivation was performed 15 DAP with the Lely®-weeder set to penetrate the soil to a depth of about 4 cm, the soil crumbled well at a driving speed of 12.2 km h^{-1}. When the potato plants were about 10 cm tall (27 DAP), the postemergence Lely®-cultivation was performed (soil penetration about 2 cm, at 11.4 km h^{-1}). The first hilling was performed

30 DAP in 1995 and 1996. In 1995 potato was hilled a second time 50 DAP, in 1996 there was no second hilling.

The weeds in four permanent 1 m^2 quadrates per plot were counted by species and developmental stage directly before each cultivation and 2 days and 1 week after each cultivation. Weed survival in potato was assumed not to be density-dependent, as cultivation was a much more important mortality factor and reduced weed density to levels with very low density-dependent mortality rates.

The survival rates for spring-tine harrowing were determined from the difference between the weed counts directly before and one week after the cultivation. In 1996 survival rates for hilling were determined using the difference between the counts directly before and one week after hilling.

Biomass production

In the studies mentioned under 'Survival in rotation crops' and 'Survival in potato' and some studies published elsewhere (Gallandt et al., 1998; Liebman et al., 1996) the weeds in the sampling quadrates were cut, sorted, dried and weighed between the end of July (rotation crops) and mid-August (potato). The ratios of weed biomass over weed density were determined by weed species and plot. To obtain density-dependent weed biomass per individual plant these data were fitted by nonlinear regressions separated by crop and year using SYSTAT 7.0, regardless of whether the regression was significant at $\alpha \leq 0.05$ (see paragraph: 'Survival in rotation crops'). The model used for the nonlinear regressions was the hyperbolic function in equation (8) with y = biomass per plant and x = density.

Seed production

Seed production was determined in rotation crops in the study described under 'Survival in rotation crops' in 1995 and 1996, and in potato in the study described in 'Survival in potato' on cultivation in potato, in 1996 only. Ten individual weeds per quadrate (i.e. 40 per plot) were sampled randomly, dried, and weighed individually and then the seeds per individual were counted. Seed number per gram of biomass was calculated. Then nonlinear regression (SPSS, 1997) was used to fit a biomass-dependent model of seed number per biomass, following the hyperbolic model in equation (8) with y = seed number per biomass and x = biomass, regardless of whether the model was significant at $\alpha \leq 0.05$ (see 'Survival in rotation crops').

Seed survival

No published data exists on the survival rates of cruciferous weed seeds at the depth increments used in the model. In addition most of the data available were obtained without exposure to predation and tillage, most likely resulting in an underestimate of natural seed mortality. Under field conditions in the study used for model validation 0.75 appears to be a conservative estimate for the annual rate of seed survival averaged over the entire soil profile from O-20 cm depth. Actual survival will be lower in most years due to delay of tillage until the spring which exposed freshly produced seed to increased winter mortality at the soil surface. Seed survival at and near the soil surface will be much lower than this average value and seed survival at greater depths will be larger than this average survival rate. The parameters used in the model are listed in Table 3.1 and

are based on estimates from Cromar et al. (1999), Donald (1993), Edwards (1980), Hails et al. (1997), Kolk (1962), Wames and Anderson (1984), and Wilson and Cussans (1975).

Table 3.1. Seed survival in the soil.
Parameters used in model. Sources for parameter estimates: Cromar et al. (1999), Donald (1993), Edwards (1980), Hails et al. (1997), Kolk (1962), Wames and Anderson (1984), Wilson and Cussans (1975), see Appendix B and Table B. 1.

depth [cm]	annual seed survival rates in the soil, for new seeds produced in wet years	dry years
0-1	0.5	0.4
1-2	0.55	0.5
2-4	0.6	0.6
4-6	0.7	0.7
6-10	0.8	0.8
10-15	0.9	0.9
15-20	0.9	0.9
0-20	0.79	0.79

Tillage parameters

Tillage parameters were adapted to the depth intervals used in our model from Cousens and Moss (1990). In addition to the primary tillage operations chisel and moldboard-plowing, modeled by Cousens and Moss (1990), seedbed preparation is simulated in our model assuming homogeneous seed distribution in the entire depth zone to which the seedbed preparation reaches (Table 3.2). Before planting potato, seedbed preparation using a disk and a spring-tooth harrow is simulated assuming even mixing of the soil to a depth of 10 cm. Before planting the rotation crops seedbed preparation using

a field cultivator is simulated assuming even mixing of the soil to a depth of 6 cm. Primary tillage is only simulated before planting of potato. Before planting of the rotation crops only seedbed preparation is simulated, but no primary tillage.

Including the Influence of Seasonal Weather Patterns in the Model

Classification of years by weather pattern

Seasonal weather patterns were classified using weekly precipitation and weekly mean temperature (Table 3.3). A season was classified as early-dry, when there were less than 20 mm weekly precipitation two and three weeks after planting (i.e. less than the 30-year average weekly precipitation for June). The weeds of the 'crucifer complex' grow rapidly at this time, if they receive sufficient water. It is also the time of emergence for potato and of rapid canopy growth in the rotation crops. A season was considered late-dry, if there was less than 21 mm weekly precipitation six and seven weeks after planting (i.e. less than the 30-year average weekly precipitation for July). The weeds of the crucifer complex are producing and filling seed at this time. For the simulations, parameters obtained in years with the weather conditions to be simulated were chosen.

The approach used here to integrate weather into the population dynamics model is an analogue to the suggestion by Colbach and Debaeke (1998) to integrate weather factors into the parameters for weed survival and fecundity by running elaborate physiological models for crop-weed interactions to determine simple parameters to be used in demographic models to keep the demographic models from becoming too complex.

Table 3.2. Tillage parameters.
From Cousens and Moss (1990) adapted to depth intervals in the model and combined with seedbed preparation, disk and spring-tooth harrow (before planting potato) mixes the soil evenly to a depth of 10 cm. A field cultivator used before planting rotation crops mixes soil evenly to 6 cm depth. The numbers in the table are the proportion of seeds moved from one depth to another depth class by the specific tillage operation.

a: moldboard-plow followed by disk and spring-tooth harrow

from depth [cm]	to depth [cm] o-1	l-2	2-4	4-6	6-10	10-15	15-20
o-1	0.0166	0.0235	0.0340	0.0460	0.0570	0.0510	0.0324
l-2	0.0166	0.0235	0.0340	0.0460	0.0570	0.0510	0.0324
2-4	0.0322	0.0470	0.0680	0.0920	0.1140	0.1020	0.065 1
4-6	0.0322	0.0470	0.0680	0.0920	0.1140	0.1020	0.065 1
6-10	0.0664	0.0940	0.1360	0.1840	0.2280	0.2040	0.1302
IO-15	0.3900	0.3700	0.3400	0.300	0.2400	0.1600	0.0664
15-20	0.4350	0.3850	0.3100	0.1320	0.1920	0.3300	0.7160

b: chisel-plow followed by disk and spring-tooth harrow

from depth [cm]	to depth [cm] o-1	l-2	2-4	4-6	6-10	IO-15	15-20
o-1	0.092	0.09	0.087	0.0774	0.0434	0.0085	0.00005
1-2	0.092	0.09	0.087	0.0774	0.0434	0.0085	0.00005
2-4	0.184	0.18	0.174	0.1548	0.0868	0.0170	0.000 1
4-6	0.184	0.18	0.174	0.1548	0.0868	0.0170	0.0001
6-10	0.368	0.36	0.348	0.3096	0.1736	0.0340	0.0002
IO-15	0.069	0.087	0.114	0.194	0.468	0.42	0.0813
15-20	0.019	0.017	0.014	0.017	0.091	0.5	0.918

c: field cultivator, no primary tillage

from depth [cm]	to depth [cm] o-1	l-2	2-4	4-6	6-10	IO-15	15-20
o-1	0.1667	0.1667	0.1667	0.1667	0	0	0
1-2	0.1667	0.1667	0.1667	0.1667	0	0	0
2-4	0.333	0.333	0.333	0.333	0	0	0
4-6	0.333	0.333	0.333	0.333	0	0	0
6-10	0	0	0	0	1	0	0
IO-15	0	0	0	0	0	1	0
15-20	0	0	0	0	0	0	1

Table 3.3. Weather conditions and classification of Presque Isle, Maine, growing seasons in the field study used for model validation.

Year	average weekly rainfall 2 and 3 WAP" [mm]	6 and 7 WAP[a] [mm]	total precipitation (May - August) [mm]	average temperature [°C]	season classification
1992	4.2	34.8	419	15.7	early dry, late wet
1993	23.5	12.3	482	15.7	early wet, late dry
1994	28.8	6.3	345	16.8	early wet, late dry
1995	13.7	6.5	219	17.9	dry
1996	28.4	30.3	390	16.2	wet
1997	29.7	4.2	449	15.5	early wet, late dry
30-year average (1967-97)	20.1	21.2	365	16.3	

[a] - WAP = weeks after planting

Model without inclusion of seasonal weather patterns

The values for the parameters used in the mean model were the means of the parameters used in the three years of the weather model determined separately for each of the crops.

Model without dens&dependence

Simulations without density-dependence were run using the same parameters as for the weather model except that simple linear conversion factors were used instead of density-dependent functions.

Validation

A six-year field study, described in Chapter 2, was used to validate the model. The study was conducted from 1992 to 1997 in the same location, it consisted of two-year potato rotations with either oat-pea-vetch, grown as green manure, or barley, grown for grain in rotation with potato. The study also contained two contrasting primary tillage practices, moldboard and chisel-plowing. Primary tillage was performed every second year in the spring prior to potato planting.

This study is independent of the model as all model parameters were obtained from separate experiments. The initial seedbank density for the simulations with the model used for validation was the mean seed density averaged over all plots planted to the same rotation crop in the validation study. The mean density of the crucifer complex seedbank happened to be larger in plots planted to oat-pea-vetch than to barley. The entire experimental field was moldboard-plowed prior to planting of the rotation crops. Since the previous history of weed infestation was unknown, the estimated densities in the lower seedbank using Knab and Hurle's (1986) findings are speculative.

A number of techniques were used to compare the results of the model simulations with the observed values from the field study. Simulations of the entire six-year period of the validation study used the initial seedbank in the field as the starting seedbank for the first year and the simulated seedbank density for the following years, thus the six simulated years were not independent of each other.

Trends in the validation simulation results are just as important as the values. To statistically compare the trends, the time-series analysis cross-correlation procedure of Systat 5 (Wilkinson, 1992) was used. Only the correlations with a time-lag of zero were

evaluated. Correlations that were greater than their associated standard error were considered significant (Box and Jenkins, 1976).

Loehle (1997) suggests that a simulation model should be evaluated using methods of hypothesis testing rather than of testing for goodness of fit. This approach was used using 95% confidence intervals around the observed field values as bounds within which the simulated values should fall if the model is to be considered indistinguishable from the real system. This method takes the variability and uncertainty of the real system into account when evaluating the model. The test statistic T was determined as follows:

T = simulated values falling within 95% CI of observed values / n) (11)

n= number of observations

If the model falls into the bounds of the real system over the entire range T = 1.0, if it falls into the bounds only over 50% of the range T = 0.5. The T statistic was determined for crucifer complex seedbank in the soil, weed density in the field and weed biomass. The T statistics for these three state variables were combined as T':

$$T' = \sum w_i T_i / \sum w_i, \quad w_i \text{ weight of T for state variable i} \qquad (12)$$

T for seedbank density was weighted with 2 as it is the best indicator for the overall population development, T for weed biomass was weighted with 2, because it usually is the state variable most closely correlated with crop yield loss (it integrates the impact of weed density and weed-crop competition), and T for weed density in the field was only weighted with 1 as this state variable is of less importance in terms of the overall development of the population and crop yield loss.

Long-term Simulations

Historical weather data for Aroostook Research Farm in Presque Isle, ME, was obtained for 20 years from 1978 to 1997. The seasons were classified as wet, dry, early-wet and late-dry, or early-dry and late-wet as above for validation. The simulations were run for 20 years using the same initial soil seedbank density as for the validation simulations and the parameters of the weather model corresponding to the types of seasons in the historical weather data.

Results and Discussion

Parameter Values

Weed seed distribution over depth for initial seedbank

Consistent with the results of a number of earlier studies (Yenish et al., 1996; Staricka et al., 1990; Knab and Hurle, 1986) weed seed density from 10-15 cm depth was greater than for shallower depths following moldboard-plowing (Table 3.4). From O-5 and 5-10 cm depth the weed seed density was very similar, most likely due to even mixing of the soil during seedbed preparation. The data from Table 3.4 were used for the initial seedbank in the population vector **p** (see Appendix A). The data for O-5 and 5-10 cm depth were divided evenly to create the depth intervals used as initial starting seedbank, because these smaller interval were needed for the simulation of seedling emergence and seed survival.

Emergence over depth

In both years of the experiment there was sufficient rain, so that moisture did not limit germination. Maximum emergence was observed one week after planting. Two weeks after planting there was still a considerable number of emerging seedlings. In all following weeks emergence was much lower (Table 3.5). In 1996, most B. rapa emerged from the top 3 cm of the soil, only a very small percentage emerged from 5 cm depth and none from below. In contrast in 1997, most seedlings emerged from the top 3 cm, but there was still considerable emergence from 5 cm depth and a low rate of germination

Table 3.4. Distribution of germinable seeds in initial seedbank.
Distribution of germinable seeds of the crucifer complex in spring of 1995 directly after moldboard-plowing and seedbed preparation with a field cultivator, directly after primary tillage (potato year). Percent of germinable seedbank from O-10 cm depth. To obtain the distribution over depth for the initial seedbanks for the simulations with the model the seed density from 0- 10 cm depth was multiplied with the percentage .

	% of seedbank	Initial seedbank for				
depth	from	--validation simulations--		other simulations		
[cm]	0- 10 cm depth	barley	oat-pea-vetch	mean	large	small
0- 10 from field		212"	466"	339"	6000	10
o-1	10	21	46	34	592	1
1-2	10	21	46	34	592	1
2-4	20	42	92	67	1183	2
4-6	20	42	93	68	1200	2
6-10	41	86	189	138	2433	4
10-15	98	208	456	332	5876	10
15-20	123[b]	260	571	416	7350	12

[a] - from Ullrich (2000), seed density from O-10 cm depth in spring 1992 before planting the first rotation crops
[b] - from Knab and Hurle (1986)

from 7.5 cm depth (Table 3.5). In 1996 emergence was observed for 6 weeks, whereas in 1997 emergence ended after 4 weeks. These results were used in the survival,

germination, and seedling development transition matrices $\mathbf{G_w}$ (see Appendix A) in the model.

Weed survival in rotation crops

In both years studied, survival of plants of the 'crucifer complex' to maturity was higher in barley than in oat-pea-vetch grown for green-manure (Table 3.6). This occurred even though 1995 was a very dry season and 1996 was a very wet season. In 1996 the survival rate in barley was greater than one, i.e. there was more late germination than mortality after the main period of emergence was over (Table 3.6). These data were used in the transition matrices for survival of seedlings to mature weeds, M (see Appendix A).

Cultivation in potato

In 1995 (very dry year) about 90% of the crucifer seedlings survived in the absence of cultivation, in 1996 (wet year) all seedlings survived without cultivation. In 1995 fewer small than medium seedlings survived spring-tine cultivation and in 1996 fewer small and medium than large seedlings survived spring-tine harrowing (Table 3.7). The higher survival rates during spring-tine harrowing in 1995 compared to 1996 were due to more aggressive harrowing in 1996 (different operator of the equipment). Small seedlings did not survive inter-row hoeing and hilling, medium and large seedlings each had higher survival rates of inter-row hoeing and hilling in 1996 than in 1995 (Table 3.7). Due to the wet weather in 1996 hilling resulted in a high rate of transplanting of weeds growing between the rows into the row. This was probably the result of the much wetter weather in 1996 that allowed for better survival and very late hilling in 1996 due to

Table 3.5. Emergence as a function of soil depth by Brassica rapa.
In 1996 8 1.2% of the seed were germinable under optimal conditions in the greenhouse, the emergence rates were used for seeds ripened in dry years. In 1997 95.6% of the seed were germinable under optimal conditions in the greenhouse, the emergence rates were used for seeds ripened in wet years. Weekly percent emergence was corrected for seeds that previously germinated.

depth [cm]	week						
	1	2	3	4	5	6	total
			1996" nercent of germinable seed[c]				
0	7.4	7.5	3.7	2.7	0	0	17.2
1	33.9	7.8	0	0	0	0	37.4
2	14.8	11.1	0	1.0	0	0	22.7
3	16.6	20.9	0	0	3.5	1.2	32.5
5	0	4.3	0	0	0	0	4.3
7.5	0	0	0	0	0	0	0.0
			1996" nercent of total seeds present[d]				
0	6.0	4.8	2.2	1.7	0	0	28.0
1	27.5	4.1	0	0	0	0	61.0
2	12.0	6.8	0	0.6	0	0	37.0
3	13.5	12.7	0	0	2.0	0.7	53.0
5	0	3.5	0	0	0	0	7.0
7.5	0	0	0	0	0	0	0.0
			1997[b] percent of total seeds present[d]				
0	35.5	8.5	4.2	4.4	0	0	46.0
1	59.0	4.9	0	0	0	0	61.0
2	73.0	16.7	4.4	0	0	0	78.5
3	69.5	33.0	0	0	0	0	76.5
5	19.5	11.2	0	0	0	0	37.3
7.5	1.5	3.0	0	0	0	0	4.5

[a] - used for seeds ripened in dry conditions
[b] - used for seeds ripened in wet conditions
[c] - used for first year of the model simulations
[d] - used for later years of model simulations

Table 3.6. Crucifer seedling survival to maturity in rotation crops.

crop	year	survival rate		density-dependent model parameters[a]				
		mean	SE[b]	a	SE[b]	c	SE[b]	type of season[c]
barley	1995	0.975	0.221	1.000	0.440	0.0070	0.0185	dry & early dry
barley	1996	1.029	0.103	1.092	0.216	0.0013	0.0039	wet & early wet
oat-pea-vetch	1995	0.859	0.109	1.000	0.224	0.0082	0.0108	dry & early dry
oat-vea-vetch	1996	0.917	0.180	0.775	0.114	0.0002	0.0054	wet & early wet

[a] - survival rate = a / (1 + c * density)
[b] - SE = standard error
[c] - indicates the type of weather the parameters were used for in model simulations

very uneven emergence of the potato crop. The data was used in the survival, germination, and seedling development transition matrices, $\mathbf{G_w}$ (see Appendix A), the differences due to operator were included in the model.

Biomass production

Generally, independent of the crop planted, the wetter the year the more biomass was produced by each individual plant of the crucifer complex (Table 3.8). Biomass per plant was greater in potato than in rotation crops. The density-dependent functions were used in the model as they prevent the population accumulating unrealistically high amounts of biomass. These results were used in the transition matrix B for the conversion from density of mature weeds to biomass of mature weeds (see Appendix A).

Table 3.7. Crucifer survival as a result of cultivations in potato.
Spring-tine cultivations were performed before emergence of potato.

Seedling Size	cultivation type	1995 survival rate mean	1995 survival rate SE"	1996 survival rate mean	1996 survival rate SE"
small	none	0.8900	0.1151	1.0000	0.0830
(cotyledon to	spring-tine harrowing	0.2887	0.0691	0.1606	0.0480
1 true leaf)	inter-row hoeing & hilling	0.0000[b]	--	0.0000	0.0000
medium	none	0.9017	0.0994	1.0000	0.0000
(2-3 true	spring-tine harrowing	0.4404	0.1365	0.1815	0.0247
leaves)	inter-row hoeing & hilling	0.0043	0.0032	0.2249	0.1447
large	none	1.0000[b]	--	1.0000	0.0000
(2 4 true	spring-tine harrowing	0.9000"	--	0.4873	0.0598
leaves)	inter-row hoeing & hilling	0.1551	0.0482	0.8501	0.1732
		dry & early dry years		wet & early wet years	

[a] - SE = standard error
[b] - no 1995 data available, used 1996 data
[c] - no 1995 data available, due to strong soil crust high survival rate of large seedlings assumed

Table 3.8. Crucifer biomass per plant as a function of crop type and crucifer density.

crop	year	biomass per plant mean [g]	biomass per plant SE[b]	density-dependent model parameters a	a SE[b]	c	c SE[b]	source [a]	used for type of year
barley	1995	0.066	0.012	1.000	12.662	0.0719	1.0388	1	dry, early dry
barley	1996	0.499	0.207	0.276	0.092	0.0026	0.0077	1	early wet
barley	1997	0.745	0.457	1.090	1.152	0.0126	0.0505	2	wet
oat-pea-vetch	1995	0.101	0.028	0.139	0.130	0.00212	0.1378	1	dry, early dry
oat-pea-vetch	1996	0.467	0.228	1.760	1.043	0.1002	0.1663	1	early wet
oat-pea-vetch	1997	0.646	0.161	0.775	0.244	0.0025	0.0045	2	wet
potato	1993	1.340	0.278	2.408	0.589	0.0132	0.0105	3	early wet
potato IL'	1995	1.054	0.331	1.789	1.453	0.1359	0.3005	4	dry, early dry
potato [d]	1996	9.234	1.671	22.989	9.837	0.1560	0.1299	4	wet

1 - rotation crop study (see 'Survival in rotation crops' in Materials and Methods)
2 - from Potato Ecosystem Study reduced input and biological pest management systems (Alford et al. 1996; Gallandt et al., 1998)
3 - from Liebman et al. (1996), extension of study in 1995 and 1996
4 - cultivation study (see 'Survival in potato' in Materials and Methods)
[a] - nonlinear regression to the hyperbolic function: biomass per plant = a / (1 + c * density)
[b] - SE = standard error
[c] - IL stands for plots subjected to one spring-tine cultivation with a Lely®-weeder
[d] - for all treatments combined

Seed production

Seed production per unit of crucifer biomass in rotation crops was lower in the dry year, 1995, than in the wet year, 1996 (Table 3.9). In potato, seed production per unit of biomass was reduced by spring-tine cultivation. Seed production per unit of biomass in potato showed no density-dependence, the data for rotation crops exhibited some density-dependence of seed production per unit of biomass. In the field data for 1995 no density-dependence could be found for seed production in barley, it was assumed that this was simply due to the high variability in the data. To include density-dependence for seed production in both rotation crops in the model, the data for all crops was fitted to the

Table 3.9. Seed production by weeds of the crucifer complex.

		seeds/biomass		density-dependent model parameters [a]				
		mean	SE[b]					
crop	year	—— no. g^{-1} ——		a	SE[b]	c	SE[b]	type of year
barley	1995	78	11	104	31	0.01	0.017	dry, late dry
barley	1996	135	8.5	no clear density dependence in data				
all crops [c]	1996			125	13	0.0003	0.0021	wet, late wet
(used for barley, wet and late wet years)								
oat-pea-vetch	1995	44	13	101	36	0.037	0.043	dry, late dry
oat-pea-vetch	1996	117	25	107	28	0.0021	0.0056	wet, late wet
potato[d]	1996	25.5	4.7	no density dependence				all years
potato NL'	1996	28.9	5.1	no density dependence				all years
potato 1L[f]	1996	25	14	no density dependence				all years
potato 2L[g]	1996	22.9	5.2	no density dependence				all years

[a] - nonlinear regression to the hyperbolic model: seed number per biomass = a / (1+ c * density)
[b] - SE = standard error
[c] - all crops are: barley, oat-pea-vetch and oat
[d] - mean of all cultivation treatments
[e] - no spring-tine cultivation
[f] - one spring-tine cultivation
[g] - two spring-tine cultivations

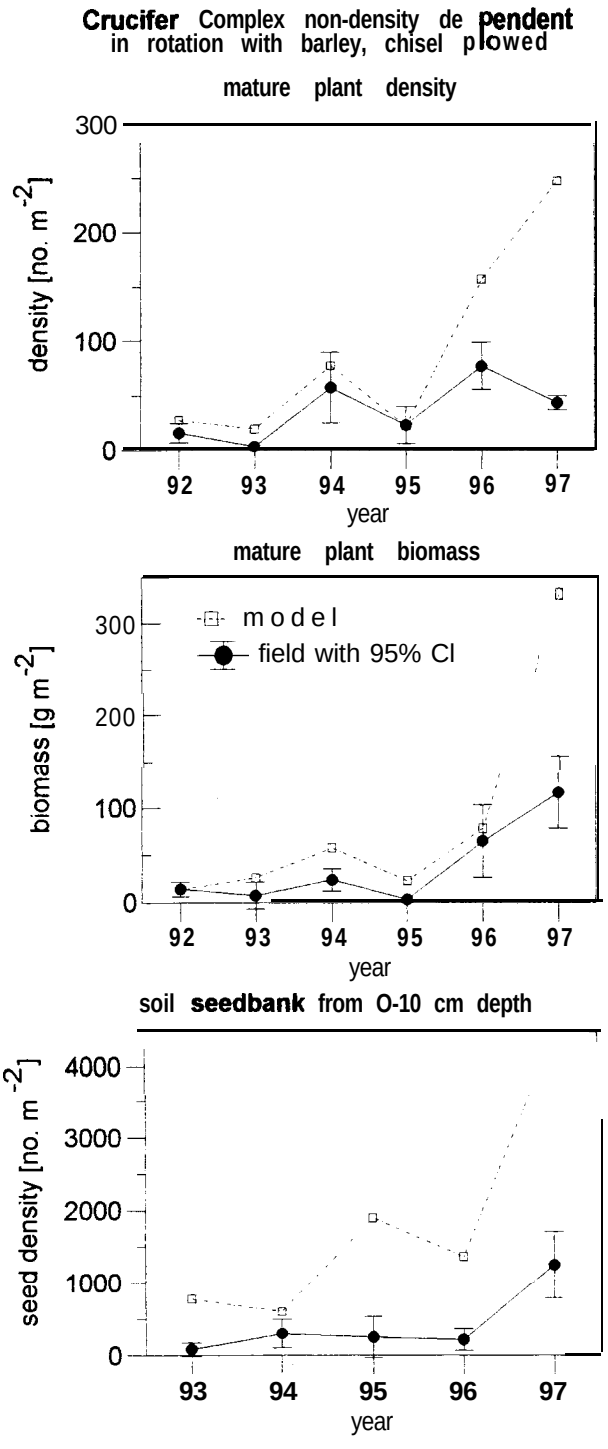
density-dependent function and used in the model for barley in wet and late-wet years (Table 3.9). These results were used in the transition matrix N for the conversion from weed biomass to number of seeds produced (see Appendix A).

Validation

The validation was initially used to identify, whether density-dependence was needed for realistic model behavior. Validation was also used to assess, whether a model that took seasonal weather patterns into account performed better than a model that used the same parameters for all years.

Non-density-dependent simulations are only presented for the treatment combination of chisel-plowing in rotation with barley, as all rotation crop and plowing treatments resulted in similar predictions. The simulation results for crucifer seedbank, plant density, and biomass were consistently greater than the field observations (Fig. 3.2). The simulated values were mostly outside the 95% confidence intervals for the field observations, with the exception of one data point for crucifer density and two for crucifer biomass. For year six, the simulation results were greater than the field observations by a factor of 5.7 for crucifer plant density, 2.9 for crucifer biomass, and 3.6 for crucifer soil seedbank. The non-density-dependent simulation results appear to increase exponentially with the exception of the dry year (1995) that results in a temporary decrease in the simulated crucifer population. To prevent unrealistic crucifer population

Figure 3.2. Crucifer complex population in a chisel-plowed, potato-barley rotation. Simulated without density-dependent functions validated against an independent field study. 95% CI = confidence interval.


Crucifer Complex non-density dependent
in rotation with barley, chisel plowed
mature plant density
density [no. m-2]
300
200
100
0
92
93
94
95
96
97
year
mature plant biomass
biomass [g m-2]
model
field with 95% CI
300
200
100
0
92
93
94
95
96
97
year
soil seedbank from 0-10 cm depth
seed density [no. m-2]
4000
3000
2000
1000
0
93
94
95
96
97
year

growth in model simulations, density-dependent functions (based on mean least error estimates from our field data) were included in the model.

The weather model (density-dependent) consistently had fewer simulated values for crucifer seedbank density, crucifer plant density and biomass outside the 95% confidence interval of the field data than the mean model (Figures 3.3 to 3.5). Consequently the statistic T (Loehle, 1997) for all three state variables individually and T' (containing all state variables weighted by importance) were higher for the weather model than the mean model (Table 3.10). The only exceptions to this were crucifer seedbank density in barley chisel-plowed treatments and crucifer plant density in oat-pea-vetch chisel-plowed treatments where the number of simulated values outside the confidence interval were equal for both model versions (Figures 3.3 to 3.5). Overall, the model predictions for biomass were more often within the confidence interval of the field data than were the predictions for the seedbank or for crucifer density (Figures 3.3 to 3.5, Table 3.10).

For a population dynamics model, predictions of the size of the population at specific points in time are important, as well as, a prediction of the oscillating population trend over time. Cross-correlation time-series analysis showed that the trends for crucifer biomass predicted by the weather model and the observed data from the field were significantly correlated (without lag) for all treatment combinations. In contrast, the predictions from the mean model were only significantly correlated with the field observations for the treatment combination oat-pea-vetch and chisel-plow. All other treatment combinations for the mean model had no significant correlations without lag (Table 3.10, Figure 3.5).

Figure 3.3. Validatibn of simulated crucifer complex seedbank.
Validated with an independent field study (density-dependent). 95% CI = confidence interval.

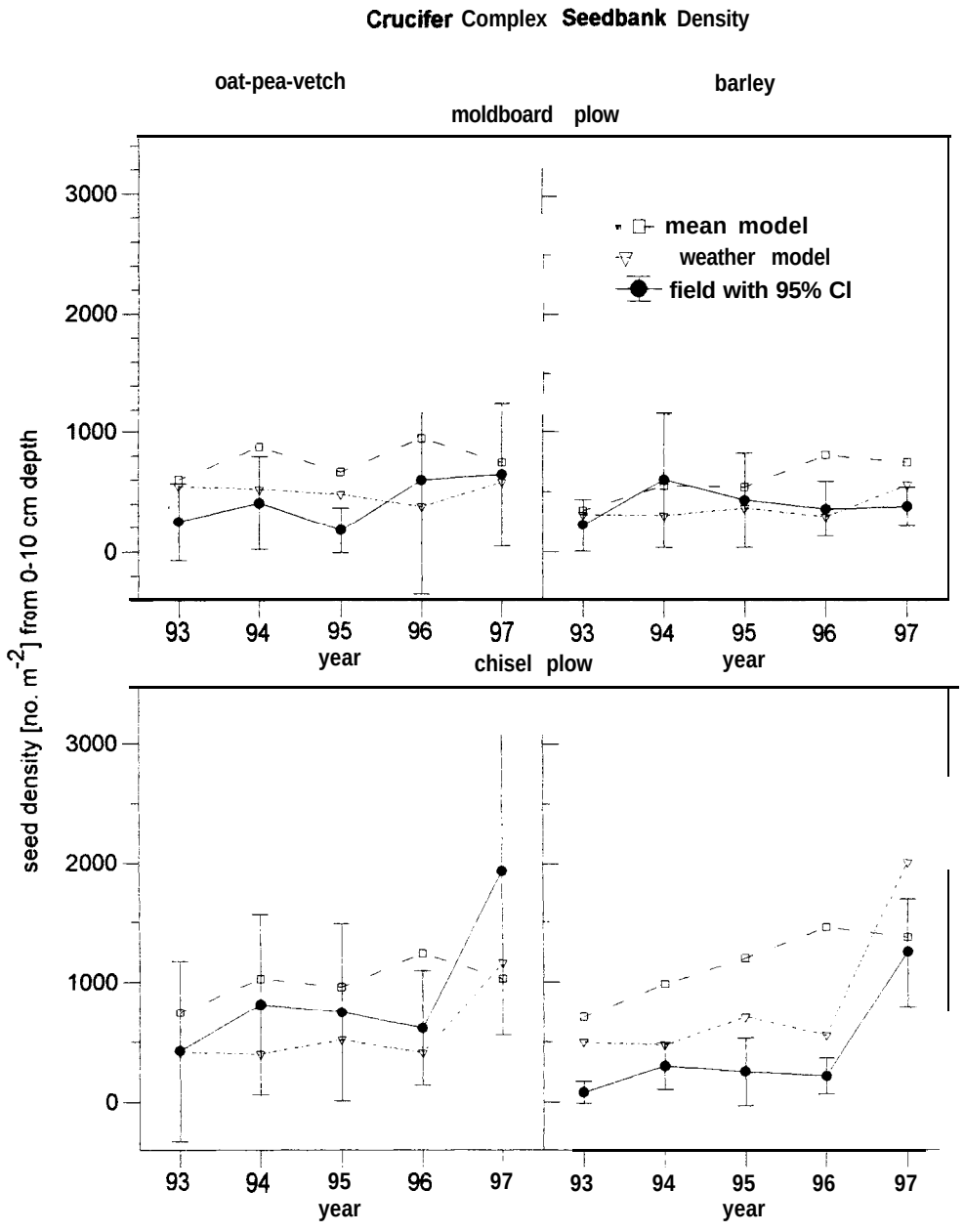

Crucifer Complex Seedbank Density
oat-pea-vetch
barley
moldboard plow
chisel plow
mean model
weather model
field with 95% CI
seed density [no. m-2] from 0-10 cm depth
3000
2000
1000
0
93
94
95
96
97
year

Figure 3.4. Validation of simulated crucifer complex density at maturity.
Validated with an independent field study (density-dependent). 95% CI = confidence interval.

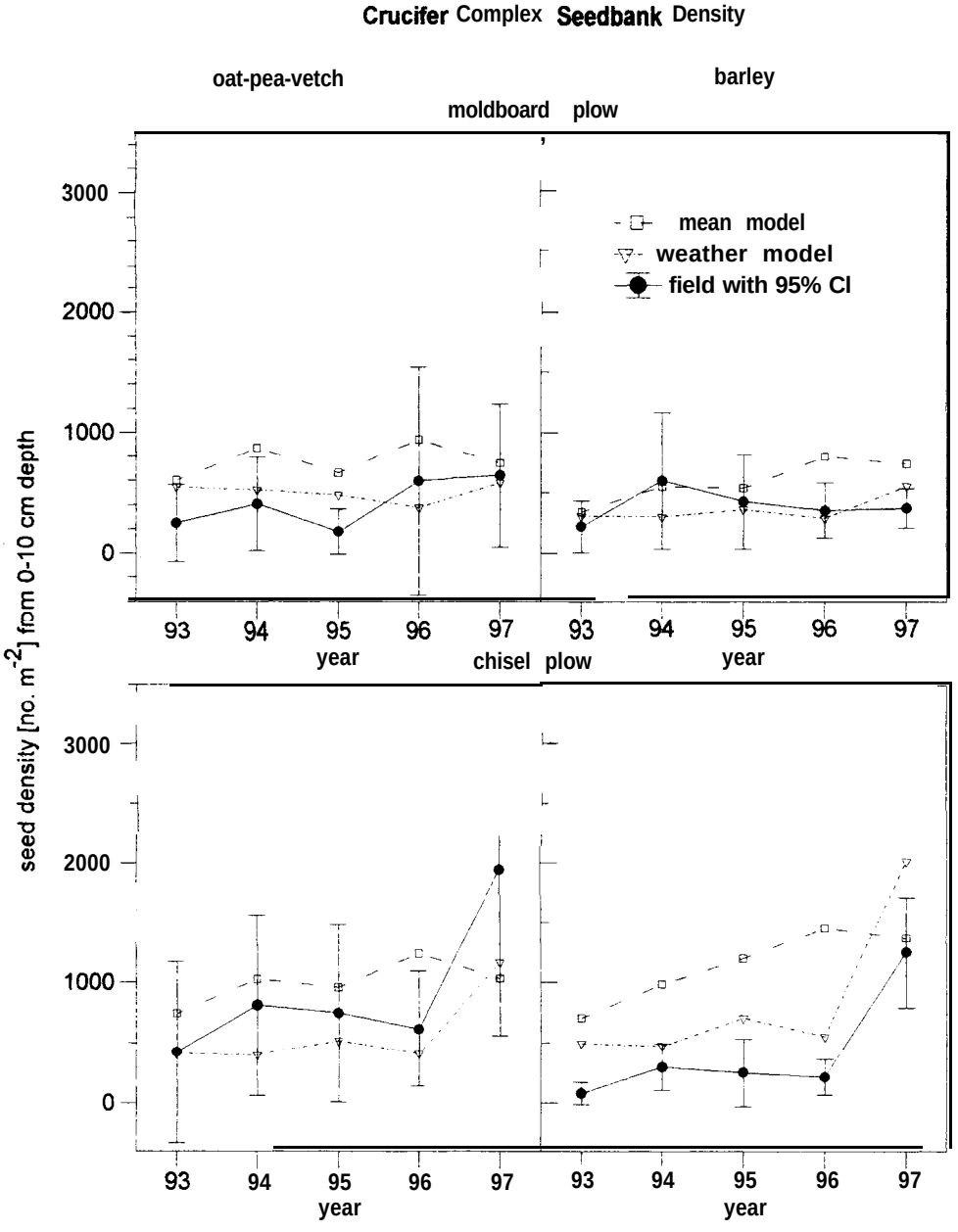

Crucifer Complex Seedbank Density
oat-pea-vetch
barley
moldboard plow
chisel plow
mean model
weather model
field with 95% CI
seed density [no. m-2] from 0-10 cm depth
3000
2000
1000
0
93
94
95
96
97
year

Figure 3.5. Validation of simulated crucifer complex biomass at maturity. Validated with an independent field study (density-dependent). 95% CI = confidence interval.

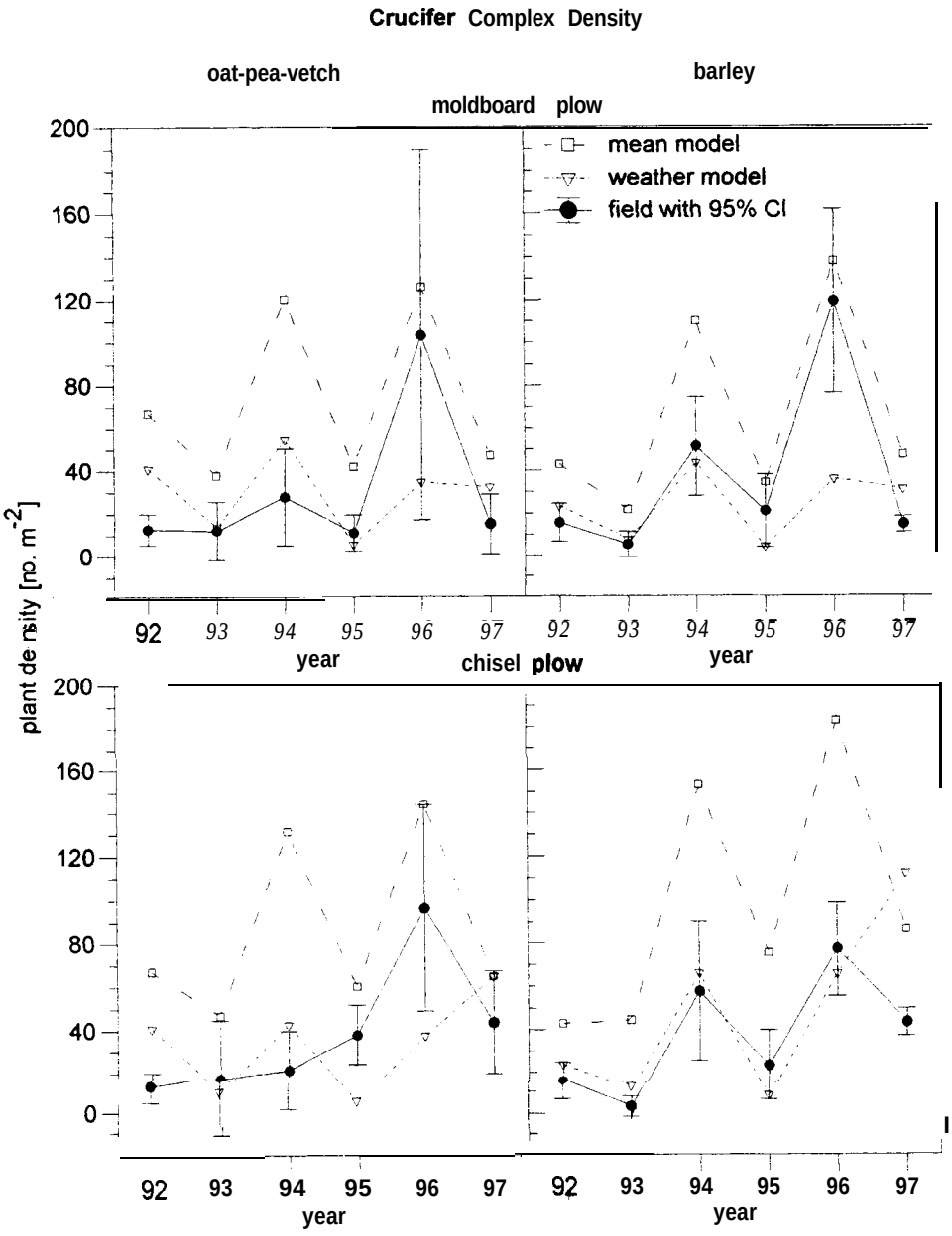

Crucifer Complex Density
oat-pea-vetch
barley
moldboard plow
chisel plow
mean model
weather model
field with 95% CI
plant density [no. m-2]
year
92
93
94
95
96
97
0
40
80
120
160
200

Table 3.10. Model validation.

Validation using simulation data that originate from continuous six-year simulations, i.e. the results for different years are dependent on each other. The simulation results are compared to a field study conducted from 1992 - 1997.

		Weather		Model		Mean		Model	
	crop	oat-pea-vetch		barley		oat-pea-vetch		barley	
state variable	tillage	chisel	mold	chisel	mold	chisel	mold	chisel	mold
		Time-Series Analysis [a]							
seedbank O-10 cm depth		0.969	ns[b]	0.981	ns	ns	0.665	0.494	ns
crucifer complex density		ns	ns	0.671	0.580	0.597	0.758	0.964	0.934
crucifer comolex biomass		0.971	0.792	0.941	0.609	0.409	ns	ns	ns
		T-Statistic [c]							
seedbank 0- 10 cm depth		1.00	0.80	0.20	0.80	0.80	0.40	0.20	0.60
crucifer complex density		0.33	0.50	0.67	0.67	0.33	0.17	0.00	0.33
crucifer comolex biomass		0.67	1.00	0.67	0.83	0.33	0.50	0.50	0.50
T' [d]		0.73	0.82	0.48	0.79	0.52	0.38	0.28	0.51

[a] - the numbers represent correlations with lag = 0 for time series analysis

[b] - ns - not significant, any correlation that was smaller than the associated standard error was considered not significant

[c] - T is the proportion of simulated data points falling within the bounds of the 95% confidence intervals of the observed field data (Loehle, 1997). When T = 1.0 the simulation cannot be distinguished from the real system.

[d] - T' was obtained by weighting T for the state variables as follows: $w_{seedbank} = 2$, $w_{density} = 1$, $w_{biomass} = 2$

The trend in crucifer density was generally better predicted by the mean model than by the weather model. In rotation with barley, the trends of both models were significantly correlated with the field trend. However, the correlation with the mean model was higher than with the weather model. In rotation with oat-pea-vetch only the trend of the mean model showed a significant correlation with the field trend. The weather model had no significant correlation (Table 3.10, Fig. 3.4).

The trend of the predicted seedbank from O-10 cm depth for chisel-plowed treatments was significantly correlated with the trend of the field observations using the weather model. The trend of the mean model predictions for oat-pea-vetch as rotation crop was not correlated with the field observations. However, with barley as the rotation crop the correlation of the trend was significant, but lower than the correlation with the weather model. In contrast, for moldboard-plowed treatments the trend of the seedbank model predictions was only significantly correlated with the mean model in rotation with oat-pea-vetch. There was no significant correlation with the trend predicted by the weather model (Table 3.10, Fig. 3.3). This comparatively poor performance of the model in predicting the seedbank for the moldboard-plowed treatment could be due to the uncertainty about the seedbank from O-20 cm depth that was not sampled in the field study.

Weed density was probably more prone to inaccurate simulation due to a lack of temperature-dependent germination and dormancy status of the seed in the model. In addition, non-density-dependent seedling mortality factors were not included in the model. This lack of accurate prediction did not get carried through to weed biomass to the same degree, as the conversion from weed density to biomass is a density-dependent

function that is also influenced by the presence of a particular crop and weather conditions. Simulated spring seedbank density is influenced by density, crop, and weather-dependent functions in the conversion from density to biomass and from biomass to seed production in the preceding year, as well as seed survival in the soil, about which there is very limited knowledge. In spite of the uncertainty in the parameters for seed survival in the soil, simulated values for the seedbank fell more frequently within the 95% CI of the field data than for density. However, the field data for seedbank density had much larger confidence intervals than did crucifer density.

For all state variables used for validation: seedbank density, weed density and weed biomass the predictions of the weather model tended to be lower than the predictions of the mean model. This was the result of dry periods accounted for in the weather model causing strong reductions in either weed density or biomass depending on when in the season the dry period occurred. The mean model lacked parameter estimates which result in low emergence, biomass and seed production that would cause intermittent declines in the weed population.

For the weather model, significant differences between treatments in the field study used for validation were, in the most part, reproduced by the model. One exception was that crucifer complex biomass in 1994 in the field was greater in barley than in oat-pea-vetch, whereas, for the weather model crucifer biomass was slightly higher in oat-pea-vetch than in barley (Chapter 2). The mean model predictions of crucifer complex biomass were opposite to the significant differences observed in the field. All other significant differences detected in the field study appeared to be reproduced by the mean model.

Validation of models of complex natural systems including crop rotations may be impossible (Oreskes et al., 1994). Differences between field observations and model predictions could easily result from some factor not included in the model such as a disease or pest infestation affecting the weed population. Since the model predicts the field observations fairly well, such factors don't seem to be of great importance during the six years of the field study used for validation. Apparently correct model predictions can result from balancing out of two or more errors within the model (Oreskes et al., 1994). This is highly unlikely to occur for our study which involves an entire six-year time-series. Jordan et al. (1995) used many hypothetical parameter values in their weed population dynamics simulation model in crop rotations and did not attempt model validation at all. Most of the parameter values used in our model are empirically derived, so validation was attempted, but the limitations to model validation should be considered.

Only a few attempts to validate weed population dynamics simulation models have been published. Zwerger and Hurle (1990) compared simulation results of the population dynamics of six weed species with field data in seven- and eight-year crop rotations dominated by winter wheat. Their validation consisted of a graphical comparison of simulated with observed seedling density in the field. They did not show the variability of the field data in their study, nor did they use any statistics for their validation. For Alopecurus myosuroides (black grass) the simulated densities were close to the field densities in all but one year when herbicides were used, even though the model did not contain a density-dependent function. When no herbicides were used in the first five years of the study the model tended to over-predict the weed density, even when

the simulation model contained density-dependent seed production. Fallopia convolvulus (wild buckwheat) populations were strongly overestimated by their model, only the overall trend was similar. The field was hand-weeded and the model assumed 80% success of the hand-hoeing of the weeds. The population dynamics of all other species were modeled without density-dependence, but included either herbicidal weed control or hand-weeding. Only the overall trends of the field populations were reproduced by the simulation results. Variation of population density from year-to-year and the population density for any particular year were not predicted well. In comparison, our weather model predicted year-to-year variability of crucifer density at maturity better, with the exception of the chisel-plowed treatment in rotation with oat-pea-vetch which performed about equally well as the model by Zwerger and Hurle (1990). The superior prediction of year-to-year variability by our model is probably due to the inclusion of weather influences. Our model predicted crucifer biomass and seedbank better than density, Zwerger and Hurle (1990) do not include these variables in their validation study.

Gonzalez-Andujar and Fernandez-Quintanilla (199 1) modeled the population dynamics of Avena sterilis (winter wild oat) in dry-land cereal cropping systems. They included density-dependent seedling survival and density-dependent seed production per plant in their model. In two simulation runs with two different herbicides in continuous winter wheat, their model reasonably described the trend of the seedbank density in the field. Significant correlations occurred between field observations and the simulated seedbank ($r = 0.92$ and 0.94, $p < 0.01$ and 0.001). A simulation of a fallow - spring barley rotation without herbicides did not correlate significantly with field observations ($r = 0.88$, $p > 0.1$). However, qualitatively, the general trend of the simulated and observed

seedbank were similar. Regardless, whether the correlation with field observations was significant, the model failed to describe the year-to-year variation in the field data. Qualitatively, our weather model performed well for the seedbank, predicting the general trend of the field data in the chisel-plowed treatments ($r = 0.97$, $p < 0.005$ oat-pea-vetch; $r = 0.98$, $p < 0.001$ barley). Our model did not predict the year-to-year variation very closely either, however this variation tended to be within the range of the annual 95% confidence intervals of the field data. The field data from the moldboard-plowed treatments did not have a clear trend over the six-year period of the validation study, consequently no significant correlation between the field observations and model predictions could be detected in the moldboard-plowed simulations.

The importance of the inclusion of weather conditions into weed population dynamics model is also supported by the findings of several other studies on demographic processes of agricultural weeds. These studies found that demographic parameters vary widely depending on seasonal weather (Fernandez-Quintanilla et al., 2000; Gonzalez-Andujar and Perry, 1995; Cousens, 1995; Forcella et al., 1992). Donald (1993) observed that B. kaber seed produced under different weather conditions had different survival rates in the soil. It has also been reported (Silverton, 1984) that dormancy patterns of seed populations produced under different environmental conditions vary, resulting in different emergence patterns in the following year. The success of mechanical weed control has been found to vary with weather conditions (Buhler, 1999).

Some of the discrepancies between our model simulations and the field observations are probably due to limitations inherent in the parameters used in the model.

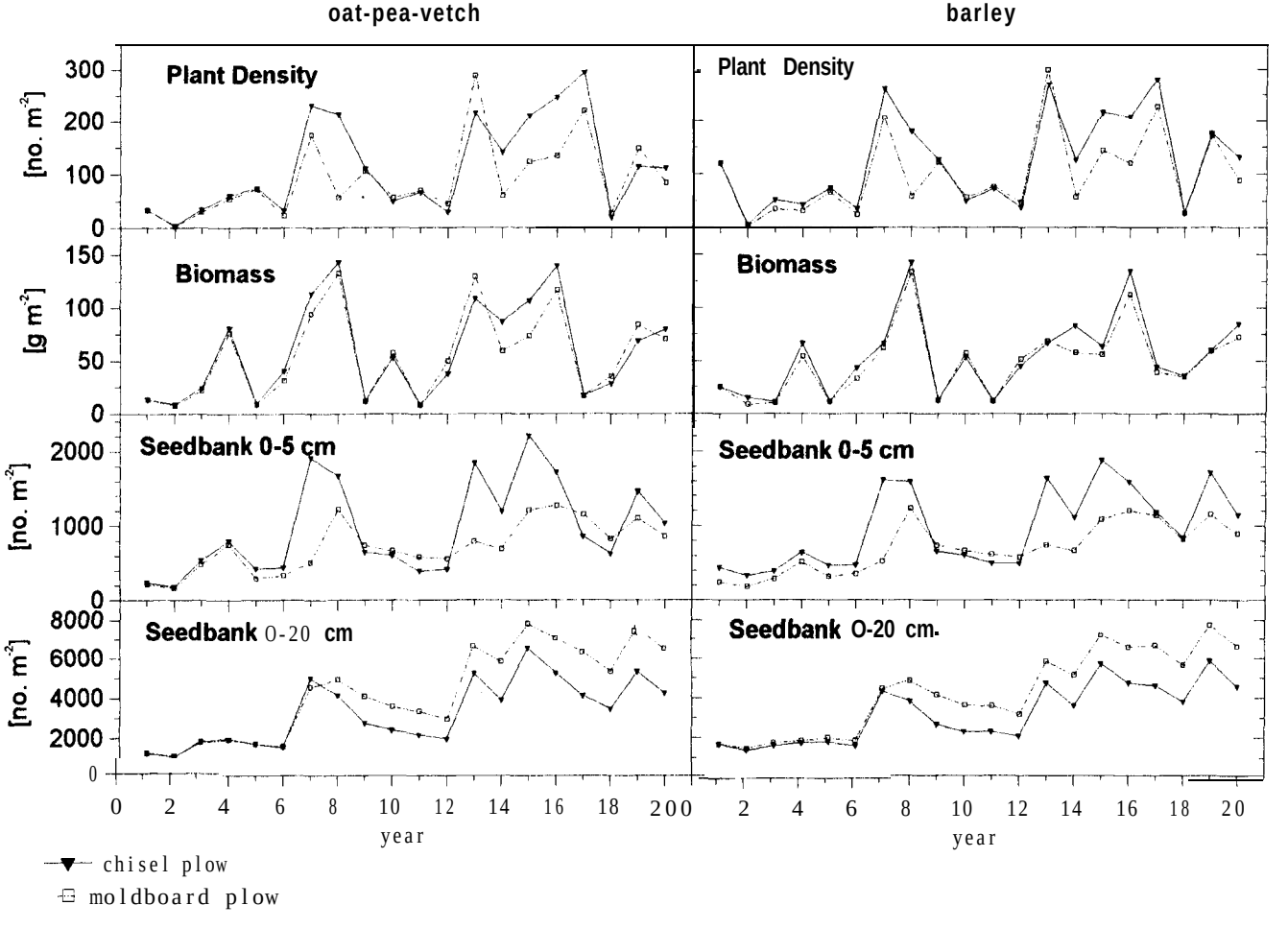
The model parameters for seed production in potato were only determined during a very wet and cold growing season, 1996, in a study mostly containing B. kaber and some R. raphanistrum, but only few B. rapa, the most abundant species of the crucifer complex in the study used for validation. In addition, the weeds sampled to determine seed production had not senesced and matured all their seeds at the time of harvest, resulting in an underestimate of total seed production. Seed survival in the soil was not measured in a field study in conjunction with this model, but only roughly estimated using published data on weed seed survival in the soil in general and B. kaber in specific. These estimates might not be accurate. Parameters for weed survival and seed production were only available for extremely wet and extremely dry years and may not represent these processes in years with relatively normal rainfall very accurately.

Overall, the predictions of the weather model were closer to the field observations than the predictions from the mean model. Consequently the weather model was chosen for the long-term simulations of northern Maine potato cropping systems.

Long-term Simulations

Overall, the predicted crucifer complex population during the 20-year simulations increased over time (Figure 3.6). The populations fluctuated strongly with seasonal weather patterns. Populations increased with wet growing seasons, decreased with dry growing seasons and remained more stable in growing seasons that were in-between the wet and dry extremes. During the past 20 years wet seasons occurred with higher

Figure 3.6. Long-term simulations with the weather model.
Using historical weather data from Presque Isle, ME from 1978 to 1997. Potato crops were simulated in even years and rotation crops in odd years.


oat-pea-vetch
barley
Plant Density
Plant Density
Biomass
Biomass
Seedbank 0-5 cm
Seedbank 0-5 cm
Seedbank 0-20 cm
Seedbank 0-20 cm.
[no. m-2]
[g m-2]
[no. m-2]
[no. m-2]
300
200
100
0
150
100
50
0
2000
1000
0
8000
6000
4000
2000
0
0 2 4 6 8 10 12 14 16 18 200
2 4 6 8 10 12 14 16 18 20
year
year
chisel plow
moldboard plow

frequency than dry seasons, resulting in the overall increase in the population. In the future, if the relative frequency of wet versus dry seasons changes due to global climate change the overall weed population trend would be expected to change as well.

Differences in crucifer biomass between years with different weather patterns within treatment combinations in the potato phase (60.0% = mean difference as percent of the overall mean for potato years) and rotation crop phase (76.1% = mean difference as percent of the overall mean for rotation crop years), were significantly greater than between treatment combinations within years (biomass in potato 15.7%, biomass in rotation crops 36.8%) at a significance level of $\alpha < 0.05$ (two sample t-test, Steele and Torrie, 1980, p. 106). Differences in crucifer density in the rotation crop phase behaved similarly (76.1% = mean difference between years with different weather conditions as percent of the overall mean, vs. 19.5% = mean difference between treatment combinations as percent of overall mean); i.e., weather conditions were more important in determining the size of the above-ground crucifer population in any given year than crop management treatment combination. The finding that weather can be more influential on weed populations than crop management treatments is supported by a study on population responses of giant foxtail and broad-leaved weeds in corn and soybean, where efficacy of mechanical control was strongly influenced by weather conditions (Buhler, 1999). Crucifer density and biomass in rotation crop years were more variable between years in oat-pea-vetch than in barley (when comparing the standard deviation as percentage of the mean over all rotation crop years for each tillage practice separately). This was probably due to higher variability between years of the weed-suppressive ability of the oat-pea-vetch green-manure than of barley (Chapter 2). In the long-term

simulation, crucifer density was lower in oat-pea-vetch relative to barley in 70% of the rotation crop years and crucifer biomass was lower in 50% of the years. In comparison, in the validation study, crucifer density was significantly lower in oat-pea-vetch than in barley in one of three years in rotation crops and crucifer biomass was significantly lower in oat-pea-vetch than in barley in two out of three years (Chapter 2).

In the predicted crucifer populations growing in the field (i.e. density of plants and biomass) no major differences between the tillage systems could be found. In rotation with oat-pea-vetch the crucifer population was larger in the chisel-plowed treatment when a series of mostly wet and early-wet years were simulated, whereas in the moldboard-plowed treatment the population was larger when a series of dry and early-dry years was simulated (Fig. 3.6). On average, the two tillage systems appeared to perform equally. In rotation with barley, chisel-plowing resulted in larger crucifer populations growing in the field than moldboard-plowing, with the exception of years 10 to 13 of the simulation, a series of dry and early-dry years, where the difference was reversed, albeit it was small (Fig. 3.6). The top five centimeters of the crucifer seedbank showed the same patterns as the above-ground crucifer population. Wet and early-wet years result in greater biomass per plant and in greater seed production per biomass than dry and early-dry years. Thus a year following a wet or early-wet year will have fewer highly viable freshly produced seeds near the soil surface when moldboard-plowed than when chisel-plowed resulting in the observed contrast between the tillage treatments. A series of dry or early-dry years following some wet or early-wet years will result in a small input of fresh seed shed. This leads to a small germinable seedbank near the soil surface following chisel-plowing. However, moldboard-plowing will bring the seeds surviving

from heavy seed shed in earlier wet years near the soil surface where they can germinate. This results in greater above-ground crucifer populations than the chisel-plowed treatment in which the soil is not inverted. The difference in tillage response between oat-pea-vetch and barley is due to higher seed production per biomass in barley compared to oat-pea-vetch (Table 3.9). This occurs even though crucifer biomass is greater in barley than in oat-pea-vetch only 50% of the time. These simulation results are consistent with the results of a model by Mohler (1993) and the results of several field experiments (Schweizer and Zimdahl, 1984; Burnside et al. 1986; Ball and Miller, 1990).

The total crucifer soil seedbank from O-20 cm depth was initially very similar in the two tillage systems. Starting with year 8 of the simulation, i.e., following two wet years with a strong population increase, moldboard-plowing resulted consistently in a larger total seedbank than chisel-plowing, as more seeds in the moldboard-plowed treatment were buried deeply where they have higher survival rates.

In the field study used to validate this model, it was found that there was no consistent difference in the ability to suppress cruciferous weeds between the two rotation crops studied (Chapter 2). This 20-year simulation indicated that even in the longer term no clear difference in weed populations results under the current climatic conditions. Considerable differences in the crucifer population size between the tillage practices were found in some years in the 20-year simulation, which again was very similar to the findings in the field study used for validation (a six-year study) (Chapter 2). The 20-year model simulations predict that the relative performance of the different treatment combinations will continue to be variable as already seen in the six-year field study (Chapter 2), however the size of the crucifer population can still increase

considerably (about three-fold for density, two-fold for biomass, and 2.5-fold for the seedbank from O-5 cm depth) compared to the population size at the end of the six-year field study (Fig. 3.6).

Summary and Conclusions

Simulation results with a version of the model containing density-dependent functions was much closer to field observations than simulation results not containing any density-dependent functions. Including weather in the model resulted in better prediction of field observations. The model predicted crucifer biomass more accurately than crucifer plant density and seedbank. Long-term simulations indicated that weather conditions influenced the size of the aboveground crucifer population more than any of the contrasting crop management practices simulated. No simulated management practice was consistently superior to the other practices simulated. It appears that the cruciferous weeds would be present in the field at levels that reduce yield considerably in most years under the management practices used in this model. This means that future research needs to concentrate on finding management practices that result in better control of cruciferous weeds. A second paper uses sensitivity analyses to identify parameters to which crucifer population dynamics are particularly sensitive and suggests areas where research into improved weed management practices should focus.

4. MODEL OF CRUCIFEROUS WEED POPULATION DYNAMICS IN POTATO-BASED CROP ROTATIONS H: SENSITIVITY ANALYSIS, EFFECTS OF WEATHER AND CULTIVATION

Abstract

Sensitivity analysis was performed on a simulation model of the population dynamics of a set of cruciferous weed species (Brassica rapa L. subsp. svlvestris (L.) Janchen, Raphanus raphanistrum L., and Brassica kaber (D.C.) L.C. Wheeler var. pinnatifida (Stokes) L.C. Wheeler) in two-year potato rotations. The size of the crucifer seedbank was most sensitive to seed survival near the soil surface, followed by seedling survival at hilling, seedling emergence in the first week after planting (WAP), and seed production in potato years. These relative sensitivities were greater with a small initial seedbank (10 m^{-2} from O-10 cm) than with a large initial seedbank (6000 m^{-2}). With a large initial seedbank, the predicted seedbank from O-10 cm depth in the soil declined over six years. With a small initial seedbank it increased. Simulations of wet years resulted in much larger crucifer populations than dry year simulations. Ranking of predicted population size between simulated treatments varied with weather conditions. Earlier hilling and two hillings, rather than a single hilling, improved simulated weed control. Spring-tine harrowing before potato emergence reduced weed density more when performed 2 WAP than 1 WAP. Postemergence harrowing reduced weeds more when performed 3 WAP than 4 WAP. The most effective cultivation regime in potato may be able to keep the crucifer population below the economic threshold in most years,

however, sole reliance on optimal timing of cultivations is not feasible, because weather conditions can prevent timely cultivation. Additional management practices need to be included in the cropping system to keep crucifers reliably below the economic threshold. Management practices that act on particularly sensitive processes in the life-cycle of the crucifers, as identified by sensitivity analysis, will probably be best suited to achieve successful crucifer management without the use of herbicides. Future research should concentrate on such management practices.

Introduction

Simulation models can be used to increase understanding of the processes influencing the dynamics of a weed population. This increased understanding can help in identifying events and processes in a weeds life-cycle that most strongly offset population dynamics. Management practices can then be developed that target these sensitive events and processes.

Jordan et al. (1995) modeled the population dynamics of Abutilon theonhrasti (velvetleaf) and Setaria viridis (green foxtail) in a four-year rotation (oat/clover-corn-soybean-corn). They used sensitivity analysis to identify the weed populations' response to changes in various parameters in their model. Similarly, Maxwell et al. (1988) modeled the population dynamics of leafy spurge (Euphorbia esula) and identified particularly sensitive transitions in its life-cycle via sensitivity analysis. Lindquist et al. (1995) used sensitivity analysis to identify factors that are particularly influential on economic optimum thresholds infestation levels for velvetleaf in corn-soybean rotations.

Jacobs and Sheley (1998) modeled the demography of spotted knapweed (Centaurea maculosa) in western rangelands and used sensitivity analysis to identify key processes influencing seed output. They found that plant survival and seed production per plant were the most influential. Once simulation models of weed population dynamics are developed, sensitivity analysis can be a powerful technique for identifying critical parameters affecting model performance and future research directions.

A large percentage of the area planted with potato in Maine (98%) and in the USA (87%) is treated with herbicides (ERS, 1997). Field studies were conducted in the potato growing region of northern Maine with the aim of reducing reliance on herbicides. When the use of herbicides was discontinued in these studies, a set of three cruciferous weed species (Brassica rapa L. subsp. svlvestris (L.) Janchen (birdsrape mustard), Raphanus raphanistrum L. (wild radish), and Brassica kaber (D.C.) L.C. Wheeler var. pinnatitida (Stokes) L.C. Wheeler (wild mustard)) became dominant (Liebman et al., 1996; Chapter 2). These three species cannot be distinguished in the seedling stage and have a fairly similar ecology, therefore they will be referred to as the "crucifer complex" from here on.

A population dynamics model for a set of cruciferous weed species in two-year potato rotations was developed and described, previously (Chapter 3). It is the most detailed purely demographic weed population dynamics model developed to date, and it contains particular detail in the depth structure of the seedbank, seedling emergence, three different seedling size classes and their differential cultivation induced rates of survival. The model simulates two alternative crops in rotation with potato, oat-pea-vetch grown as green-manure and barley grown for grain. It also simulates two contrasting

primary tillage practices, moldboard and chisel-plowing. Primary tillage is simulated once every two years in the spring before planting potato. The model has been validated with data from an independent six-year field study (Chapter 2).

In this paper the model of the population dynamics of the crucifer complex in potato rotations (Chapter 3) is subjected to sensitivity analysis. The results of the sensitivity analysis are discussed in relation to the natural variability found in estimates of the parameters in the model. We also used the sensitivity analysis to identify important uncertainties in parameter estimates representing key weed population dynamic processes that may require more research, and to identify where research on alternative weed management practices should focus.

In long-term simulations with this model, weather was an influential factor on crucifer population dynamics (Chapter 3). To further study the impact of weather conditions on the behavior of simulated crucifer populations, a number of different seasonal weather conditions were simulated for six-year periods.

Cultivation is a powerful weed management practice in potato production systems that was used successfully long before herbicides became available (Lutman, 1992). Light-weight spring-tine harrows were developed in the last few decades and can be used both between rows and over rows, preemergence, as well as, during the early postemergence period of potato growth. Their use typically results in improved weed control especially within the row (Graf et al, 1993). Timing of these spring-tine cultivations is critical because small weed seedlings are much more likely to be killed by this practice than larger seedlings (Chapter 3). The model was used to identify the impact

of different frequencies and timings of spring-tine cultivations and hilling on the population dynamics of the crucifer complex.

Materials and Methods

Sensitivity Analysis

Sensitivity analysis was performed by changing one parameter at a time while all others were kept constant.

Relative sensitivity with an average initial seedbank

The same starting seedbank was used for all sensitivity analysis treatment combinations. The initial seedbank used was the mean of the starting seedbank measured in the field in the study used for validation (Chapter 2) with 278 readily germinable seeds m^{-2} from O-10 cm depth and 1026 m^{-2} from O-20 cm depth. The relative sensitivities were determined by increasing and decreasing the value of the tested parameter by 10% and running simulations over six years with these altered parameters. The mean of the percent change in the state variable of interest compared to the model outcome with the original unchanged parameter is the relative sensitivity (Caswell, 1989):

$$\text{Relative Sensitivity} = \{ [\text{abs}(x - x_{-10\%}) / x] + [\text{abs}(x - x_{+10\%}) / x] \} / 2 \quad (1)$$

x - simulated value of state variable of interest with original parameter,

$x_{-10\%}$ - simulated value of state variable of interest with parameter decreased by 10%,

$x_{+10\%}$ - simulated value of state variable of interest with parameter increased by 10%.

Not all parameters of the model were included in the sensitivity analysis. Analyses were restricted to those parameters that can either be influenced by management practices or that vary considerably due to changes in environmental conditions. Seed survival near the soil surface (O-l cm depth) was chosen as it is believed to be particularly variable in response to both environmental conditions and management practices (Brust and House, 1988; Roush et al., 1989).

The relative sensitivity of the crucifer seedbank, crucifer plant density and biomass in potato years to seedling emergence of the crucifer complex was tested by changing the emergence rate during the first week after planting for all depth intervals in the soil, and by changing the emergence rate from 0 to 4 cm depth effective throughout the entire period of crucifer emergence. Weeds emerging before the crop tend to be the most damaging (O'Donovan et al., 1985), and for the species complex studied, a large proportion of the weeds emerging did so during the first week after planting (Chapter 3). The majority of these cruciferous weeds emerged from the top 4 cm of soil (Chapter 3). Thus, emergence from the top 4 cm could be an influential factor. The parameters mentioned above are involved in every year of the model simulations.

The following parameters are involved only every second year of the model simulations, either only in potato or only in rotation crop years. Crucifer survival in potato years in response to spring-tine cultivation and hilling were chosen because the success of these mechanical weed control practices can vary considerably with the timing

of cultivations, operator skill, as well as with weather conditions at the time of cultivation. It is important, therefore, to identify how influential these cultivations are on crucifer infestation in potato and on overall crucifer population dynamics. Weed mortality in potato is dominated by mortality due to cultivation rather than natural mortality (Chapter 3), therefore, natural mortality was not included in the parameters for which relative sensitivity was determined.

In rotation crop years, the relative sensitivity of model output to parameters in three density dependent functions was determined. These parameters were crucifer seedling survival to maturity, biomass production per individual crucifer plant and seed production per gram biomass of cruciferous weeds. The conversions are density dependent functions of the form:

$$f(n_2) = a / [1 + c * n_1] \qquad (2)$$

if n_1 is the density of crucifer seedlings, n_2 is the density of mature cruciferous weeds,

if n_1 is density of mature cruciferous weeds, n_2 is crucifer biomass,

if n_1 is crucifer biomass, n_2 is number of crucifer seeds produced.

a = maximum value for $f(n_2)$, c = parameter for density dependence

Sensitivity analysis was performed for the parameters c. The parameters c were chosen for sensitivity analysis, because they have large standard errors (Chapter 3). This high degree of uncertainty in the parameters c in the model would be problematic, if the model outcome were to respond sensitively to changes in these parameters. In potato years the relative sensitivity to the parameters for the same conversions was determined, but only the conversion from crucifer density to biomass was modeled as a density

dependent function. The conversion from biomass to seed production was a density independent parameter. Therefore, only the parameter c was used in sensitivity analysis in the conversion to biomass.

Crucifer density and biomass in potato years were used as state variables to measure the changes due to the increased and decreased parameters in sensitivity analysis. They are measures of infestation with cruciferous weeds in potato that could result in yield loss. Potato is of much greater economic importance in these rotations in northern Maine than are the rotation crops, therefore only potato years were chosen for this analysis. To account for years with different weather conditions, the mean of the relative sensitivities found in the second and third cycle of the three cycle rotation simulations was reported.

To determine relative sensitivity, the simulation results of crucifer seedbank from O-10 and from O-20 cm depth in the spring following the last rotation crop (year 5) and the last potato year (year 6) were used. The mean of the relative sensitivity of these two years was reported. The seedbank from O-10 cm depth was chosen as an indicator of the potential weed population and the seedbank from O-20 cm depth was chosen as an indicator of the overall weed population, as it contains all individuals within the population in the spring before germination begins.

Variability in Data Used for Parameters

The natural variability in the model parameters was determined in order to relate the variation between treatments and years and within the same treatment and year to the results of the sensitivity analysis. Different types of variability were determined as follows:

Percent difference between contrasting treatments =

$$100 \times (\text{treatment}_1 - \text{treatment}_2) / \text{mean of both treatments} \quad (3)$$

Percent difference between different years =

$$100 \times (\text{treatment mean year}_1 - \text{treatment mean year}_2) / \text{mean of both years} \quad (4)$$

Percent variability within treatment and year =

$$100 \times SE / \text{mean} \quad (5)$$

Relative Sensitivity with Large and Small Initial Seedbank

Relative sensitivity to the different parameters used in the model might be dependent on the initial conditions of the system. A small initial seedbank of 10 seeds m^{-2} from O-10 cm depth (32 seeds m^{-2} from O-20 cm depth) was chosen. This density is representative of a small initial population of a weed species that has recently colonized a new field or a small remaining seed population left in a field that did not support reproduction of the weed species for many years. Also, a large initial seedbank of 6000

seeds m^{-2} from O-10 cm depth (19226 seeds m^{-2} from O-20 cm depth) was chosen. This is a typical number for a weed species that occurs at high densities in agricultural fields (Schweizer and Zimdahl, 1984). Relative sensitivities reported are for the results of the last rotation cycle in a six-year simulation, as an indicator of the general trend of the crucifer population.

The number of parameters for which the relative sensitivity was determined was reduced compared to the sensitivity analysis with the mean starting seedbank. Only one of the parameters for emergence was used, emergence in the first week, as it had higher relative sensitivity in our initial sensitivity analysis. Only one parameter for crucifer survival in potato, survival at hilling, was included, which was the more influential parameter in our initial sensitivity analysis. For the density dependent conversions of weed density to biomass and of biomass to seed number, the parameter with the higher relative sensitivity in the initial sensitivity analysis was used. For potato years, seed production per unit of total aboveground biomass was used and for rotation crop years, biomass per weed was used in the sensitivity analysis.

Simulations with Large and Small Initial Seedbank

Six-year simulations with the seasonal weather patterns that characterized the field study used for validation (Chapter 2) were run for all treatment combinations using the same small (10 readily germinable seeds m^{-2} from O-10 cm depth) and large (6000 readily germinable seeds m^{-2} from O-10 cm depth) initial seedbank. The objective of these simulations was to see what impact different initial seedbank densities have on

model performance, and to identify whether there are any differences between the performance of the different treatment combinations with these contrasting initial seedbanks.

Weather Simulations

The validation of the model (Chapter 2) indicated that seasonal weather patterns strongly influence model output and actual field data. In order to identify how different seasonal weather patterns over a six-year period influence the simulation outcome, a number of simulations were run with different seasonal weather patterns. All four types of seasons (wet, dry, early-wet/late-dry, and early-dry/late-wet (Chapter 3) were simulated for six consecutive years each. In addition, three wet years followed by three dry years and three dry years followed by three wet years were also simulated. The weather simulations were run with the mean of the initial seedbank estimates from the field study as used in sensitivity analysis.

Cultivation Simulations

The cultivation simulations were only performed for the treatment combination of oat-pea-vetch as rotation crop and chisel-plowing as primary tillage. Preemergence spring-tine cultivations were simulated one or two weeks after planting and postemergence spring-tine cultivations were simulated three or four weeks after planting. Simulations with only one spring-tine cultivation were only run for preemergence cultivations. Crucifer seedling survival rates during postemergence spring-tine harrowing

were determined in the field study described in Chapter 3. The crucifer seedling survival rates for postemergence spring-tine harrowing were 0.16 for small seedlings (cotyledon to 1 true leaf), 0.51 for medium seedlings (2 to 4 true leaves), and 0.57 for large seedlings (> 4 true leaves) (only determined in the wet 1996 season). Hilling was simulated for four, five, or six weeks after planting (WAP) with individual simulation runs containing one or two hillings. These are all typical timings for cultivation and hilling in potato.

Results and Discussion

Sensitivity Analysis

A relative sensitivity of one means that a 10% change in the parameter studied resulted in a 10% change in a state variable in the outcome of the simulation. A relative sensitivity smaller than one indicates that the state variable in the simulation outcome changed by less than 10%. A relative sensitivity greater than one indicates that the state variable in the simulation outcome changed by more than 10% due to the 10% change in the parameter used in the simulation. In the following discussion values of relative sensitivity will be grouped by range as follows: low (< 0.5), moderate (0.5 to 1.0) and high relative sensitivity (≥ 1).

All state variables responded with much higher sensitivity to all parameters tested when a small initial seedbank was used than when a large initial seedbank was used (Table 4.1). The very high sensitivity with a small initial seedbank can easily be explained. When only a few seeds are produced with a small initial seedbank they contribute a large proportion of all the seeds present. In contrast, with a large starting

seedbank any changes have to be large in order to result in any large proportional changes in the soil seedbank. The sensitivity analysis using the initial seedbank measured in the field of the study used for validation resulted in relative sensitivities intermediate between these two extreme seed densities in the soil seedbank (Tables 4.1, 4.2 and 4.3).

Lindquist et al. (1995) conducted sensitivity analysis on the economic optimum threshold density for A. theophrasti in corn-soybean rotations with two different initial seedbank densities of 1 and 100 seeds m^{-2} and found only slight differences between the results. In contrast, in our study there were fairly large differences in the relative sensitivities and some differences in the order of importance of the parameters between the small and large initial seedbank density tested. However, the difference in the size of the initial seedbank in our study was much larger with initial densities of 10 and 6000 m^{-2} for 0- 10 cm depth.

Only the results of sensitivity analysis on individual factors will be presented here, as sensitivity analysis on three-way interactions between weed seed survival in the top centimeter of the soil with weed survival during hilling and during spring-tine cultivation did not indicate any interactions. Analysis for two-way interactions between weed seed survival in the top centimeter of the soil with the exponential parameter in the density dependent biomass production per weed in the rotation crop phase also did not result in the detection of interactions of any practical importance.

Table 4.1. Relative sensitivity of crucifer populations with high and low initial seedbanks to ± 10% changes in selected parameters.

Parameter changed	low initial seedbank 10 m^{-2} from O-l 0 cm depth															
	----relative sensitivity of crucifer plants in potato[a]---------relative sensitivity of the crucifer seedbank[b]--------															
	-----crucifer density-----				-----crucifer biomass-----				----- 0- 10 cm depth-----				----- O-20 cm depth-----			
Rotation crop	oat-pea-vetch		--barley--		oat-pea-vetch		--barley--		oat-pea-vetch		--barley--		oat-pea-vetch		--barley--	
Tillage practice	Ch[c]	M[d]	Ch	M	Ch	M	Ch	M	Ch	M	Ch	M	Ch	M	Ch	M
seed survival O-l cm soil depth"	2.68	1.44	2.82	1.5	2.48	1.41	2.34	1.46	3.62	2.1	3.39	2.31	3.36	2.09	3.28	2.27
emergence in week 1[e]	2.26	1.58	2.32	1.57	2.10	1.55	1.94	1.53	2.00	1.19	1.77	1.27	1.85	1.19	1.71	1.25
plant survival in potato years hilling	1.79	1.50	1.78	1.34	1.66	1.47	1.49	1.31	1.25	0.96	1.06	0.83	1.15	0.80	1.01	0.64
in potato seed production per g biomass	0.81	0.51	0.81	0.35	0.74	0.50	0.67	0.34	1.31	0.97	1.17	0.85	1.20	0.81	1.12	0.65
in rotation crop biomass per weed[f]	0.11	0.07	0.15	0.07	0.10	0.07	0.12	0.07	0.11	0.08	0.18	0.08	0.10	0.08	0.18	0.08
	high initial seedbank 6000 m^{-2} from O-IO cm depth															
seed survival O-l cm soil depth'	1.07	0.25	1.06	0.28	0.51	0.09	0.50	0.10	1.51	0.55	1.26	0.56	0.42	0.58	0.41	0.54
emergence in week 1"	0.90	0.74	0.86	0.73	0.47	0.32	0.43	0.31	0.27	0.06	0.08	0.08	0.07	0.04	0.02	0.22
plant survival in potato years hilling	1.19	1.03	1.12	1.02	0.66	0.44	0.58	0.43	0.30	0.09	0.17	0.08	0.08	0.06	0.05	0.05
in potato seed production per g biomass	0.31	0.07	0.23	0.07	0.16	0.03	0.12	0.03	0.57	0.30	0.39	0.29	0.15	0.16	0.12	0.13
in rotation crop biomass per weed'^	0.20	0.05	0.39	0.11	0.11	0.02	0.15	0.04	0.21	0.07	0.39	0.14	0.06	0.12	0.13	0.25

[a] - averaged over the second and third potato year of six year simulations
[b] - averaged over the last rotation crop and potato year in six year simulations
[c] - Ch - chisel plowed [d] - M - moldboard plowed
[e] - parameters changed in all years
[f] - density dependent function: biomass = a / (1 - c * density), the parameter c was used for sensitivity analysis

Table 4.2. Relative sensitivity of the crucifer seedbank.

Relative sensitivity to + and - 10% changes in selected parameters with an average initial seedbank (339 seed m^{-2} from O-10 cm depth) averaged over the last two years of six year simulations. The numbers in brackets are the ranks for the relative sensitivity in each treatment.

Parameter- changed	Relative Sensitivity of the Crucifer Seedbank									
	0-10 cm depth					0-20 cm depth				
Rotation crop	---oat-pea-vetch----		--------barley--------		rank of	---oat-pea-vetch---		——— barley --------		rank of	rank of overall
Tillage practice	Chisel	Mold	Chisel	Mold	mean	Chisel	Mold	Chisel	Mold	mean	mean
seed survival O-l cm depth[a]	2.24 (1)	1.50 (1)	1.88 (1)	1.61 (1)	1	1.68 (1)	1.36 (1)	1.59 (1)	1.47 (1)	1	1
emergence (all years)[a]											
in week !	0.74 (3)	0.54 (5)	0.41 (5)	0.53 (5)	4	0.54 (3)	0.52 (3)	0.36 (5)	0.51 (2)	3	3
from O-4 cm depth	0.67 (5)	0.48 (6)	0.38 (6)	0.47 (6)	6	0.50 (4)	0.48 (4)	0.34 (6)	0.46 (4)	4	5
plant survival in potato years											
hilling	0.70 (4)	0.69 (3)	0.45 (3)	0.64 (3)	3	0.50 (4)	0.44 (5)	0.37 (4)	0.40 (5)	5	3
spring-tine cultivation	0.51 (6)	0.60 (4)	0.36 (8)	0.58 (4)	5.	0.36 (6)	0.30 (6)	0.30 (7)	0.29 (7)	6	6
in potato											
biomass per weed[b]	0.30 (7)	0.20 (7)	0.37 (7)	0.25 (8)	7	0.21 (8)	0.09 (9)	0.27 (8)	0.11 (8)	8	8
seed production per unit biomass	1 .oo (2)	0.88 (2)	0.82 (2)	0.90 (2)	2	0.71 (2)	0.53 (2)	0.64 (2)	0.51 (2)	2	2
in rotation crop											
survival[b]	0.05 (10)	0.03 (10)	0.07 (9)	0.04 (9)	10	0.04 (10)	0.04 (10)	0.06 (9)	0.04 (9)	10	10
biomass per weed[b]	0.28 (8)	0.15 (8)	0.43 (4)	0.26 (7)	7	0.23 (7)	0.16 (7)	0.39 (3)	0.37 (6)	7	7
seed production per unit biomass[b]	0.18 (9)	0.09 (9)	0.05 (10)	0.03 (10)	9	0.14 (9)	0.10 (8)	0.04 (10)	0.03 (10)	9	9

[a] - parameter changed in every year of the simulation runs

[b] - changed parameter c in a density- or biomass-dependent function of the form: $y = a / (1 - c*x)$

Table 4.3. Relative sensitivity of crucifer plant density and biomass in potato.

Relative sensitivity to + and - 10% changes in selected parameters with an average initial seedbank (339 seed m^{-2} from 0-10 cm depth) averaged over the last two years of six year simulations. The numbers in brackets are the ranks for the relative sensitivity in each treatment.

Parameter changed	Relative Sensitivity of Crucifer Density and Biomass in Potato										
	crucifer density					crucifer biomass					rank of
Rotation crop	oat-pea-vetch		barley		rank of	oat-pea-vetch		barley		rank of	overall
Tillage practice	Chisel	Mold	Chisel	Mold	mean	Chisel	Mold	Chisel	Mold	mean	mean
seed survival 0-1 cm depth[a]	1.69 (1)	0.72 (4)	1.84 (1)	0.96 (3)	1	1.17 (1)	0.58 (4)	1.15 (1)	0.73 (3)	2	1
emergence[a]											
in week 1	1.29 (3)	0.98 (2)	1.35 (3)	1.07 (2)	3	0.92 (3)	0.82 (2)	0.96 (2)	0.83 (2)	3	3
from 0-4 cm depth	1.11 (4)	0.83 (3)	1.15 (4)	0.91 (4)	4	0.79 (4)	0.70 (3)	0.73 (4)	0.71 (4)	4	4
plant survival in potato years											
hilling	1.34 (2)	1.16 (1)	1.38 (2)	1.21 (1)	2	0.98 (2)	0.97 (1)	0.89 (3)	0.95 (1)	1	1
spring-tine cultivation	0.79 (5)	0.68 (5)	0.89 (5)	0.75 (5)	5	0.51 (5)	0.45 (5)	0.49 (5)	0.53 (5)	5	5
in potato											
biomass per weed[b]	0.03 (10)	0.02 (10)	0.07 (10)	0.03 (9)	10	0.28 (6)	0.17 (6)	0.41 (6)	0.23 (6)	6	8
seed production per unit biomass	0.37 (7)	0.17 (6)	0.46 (7)	0.24 (7)	7	0.25 (8)	0.14 (7)	0.30 (8)	0.18 (8)	8	7
in rotation crop											
survival[b]	0.05 (9)	0.04 (9)	0.08 (9)	0.04 (8)	9	0.04 (10)	0.04 (10)	0.05 (10)	0.03 (9)	10	10
biomass per weed[b]	0.38 (6)	0.14 (7)	0.55 (6)	0.30 (6)	6	0.28 (6)	0.11 (8)	0.32 (7)	0.23 (6)	7	6
seed production per unit biomass[b]	0.72 (8)	0.09 (8)	0.09 (8)	0.03 (9)	8	0.18 (9)	0.07 (9)	0.06 (9)	0.02 (10)	9	9

[a] - parameter changed in every year of the simulation runs

[b] - changed parameter c in a density- or biomass-dependent function of the form: $y = a / (1 - c*x)$

Seed survival near the soil surface

The crucifer seedbank had the highest relative sensitivity to seed survival in the top centimeter of the soil (Table 4.2). When the seedbank from O-10 as well as from O-20 cm depth was used as the variable to evaluate sensitivity, this parameter was by far the most influential parameter for all rotation crop and tillage practice combinations. Generally the soil seedbank from O-10 cm depth was more sensitive to changes in seed survival near the soil surface than the seedbank from O-20 cm depth (Table 4.2).

With a very small initial seedbank, as well as with a large initial seedbank, the relative sensitivity of the seedbank was also highest to seed survival in the top centimeter of the soil (Table 4.1). With a small initial seedbank the relative sensitivity to this parameter was very high (Table 4.1). With a large initial seedbank the relative sensitivity of the seedbank from O-10 cm depth was moderate to high (Table 4.1) and of the total seedbank from O-20 cm depth it was low to moderate (Table 4.1).

Crucifer plant density and biomass in potato was most sensitive to seed survival near the soil surface for chisel-plowed treatments (Table 4.3). In contrast, in moldboard-plowed treatments, crucifer plant density and biomass were most sensitive to the parameter for weed survival at hilling (Table 4.3).

With a small initial seedbank, seed survival from O-l cm depth was also the most influential factor on crucifer density and biomass in potato in chisel-plowed treatments, followed by the emergence rate in the first week after planting (Table 4.1). In moldboard-plowed treatments seed survival from O-1 cm depth in the soil was only the second most influential parameter, however, its relative sensitivity was close to the relative sensitivity

of the most influential parameter, the emergence rate in the first week after planting (Table 4.1).

With a large initial seedbank in chisel-plowed treatments, seed survival from O-l cm depth was only the second most influential parameter on crucifer density and biomass in potato years after seedling survival at hilling. For moldboard-plowed treatments the sensitivity of crucifer density and biomass in potato to seed survival near the soil surface was low and only the third most influential factor following emergence in the first week after planting (Table 4.1).

All state variables tested were more sensitive to seed survival in the soil in chisel-plowed treatments than in moldboard-plowed treatments. This was expected, because chisel-plowing leaves seeds on and near the soil surface near the soil surface where they can germinate successfully, whereas moldboard-plowing turns most of the seeds that initially are near the soil surface under moving them to depths where they cannot germinate successfully and bringing seeds from deeper in the soil closer to the surface (Mohler, 1993). Thus with moldboard-plowing the total seed density from O-20 cm depth will still be reduced due to low seed survival near the soil surface, but this parameter will have a smaller effect on the density and biomass of crucifers in the field and consequently on crucifer seed production and the overall population development.

Seed survival near the soil surface was also identified as the most influential parameter in a simulation study by Jordan et al. (1995). They simulated the population dynamics of two contrasting weed species, A. theophrasti (long-lived seeds) and Setaria viridis (short-lived seeds), in corn-soybean rotations. Seed survival near the soil surface

thus appears to be a highly influential factor for weed population dynamics across weed species and across cropping systems. Lindquist et al. (1995) identified A. theophrasti seed survival in the soil to be the third most influential factor on the economic optimum threshold density after seedling survival and reduction in seed production, both due to herbicides, i.e., aside from herbicides seed survival was the most influential factor in their study. In the study by Jordan et al. (1995) and in our study herbicides were not used. The importance of seed mortality was also stressed by Hickman (1979), who stated that more than 95% of all plant mortality occurs during the seed stage.

A number of studies have focused on specific factors influencing seed survival in the soil; most of them, however, require further research and development before they can be applied successfully in farmers' fields. A number of studies state that the depth of seed burial is an important factor in seed survival in the soil (e.g.: Reeves et al., 1981; Taylorson, 1970; Mohler and Galford, 1997). Thus, tillage can affect seed survival in the soil by influencing depth of burial; frequency of soil disturbance can affect seed survival by stimulating germination (Roberts and Feast, 1973); timing of tillage determines the length of time the seeds remain on the soil surface exposed to mortality factors, such as seed predators (Brust and House, 1988; Zhang et al., 1997). The types of crops used in a rotation are also likely to affect seed survival, as many seed predators have been found to be more active in fields with cover crops or substantial crop residues remaining on the soil surface following weed seed shed (Zhang et al. 1997). Other approaches, such as application of microbes (Kremer, 1993) and soil solarization (Egley, 1990), have been shown to reduce seed survival in the soil.

Only the relative sensitivity to seed survival in the soil from O-l cm depth was determined in our study and found to be highly influential on the crucifer population. This means overall seed survival in the soil is of even greater importance, because there are many more seeds in the soil than just in the top centimeter and the survival rates for seeds in the soil increase only gradually with increasing depth of burial (Chapter 3).

Considering the high relative sensitivity of the seedbank, plant density and biomass of annual weeds to seed survival in the soil, the development of management practices that can reduce weed seed survival should receive increased research efforts.

Emergence

The relative sensitivity of the crucifer seedbank to changes in the emergence rate during the first week after planting was low to moderate (Table 4.2). It occupied the third rank for parameters influential on the weed seedbank, after crucifer seed production per unit of biomass in potato years (moderate relative sensitivities, Table 4.2). The difference between years for emergence during the first week after planting was high (Table 4.4). Emergence from the top 4 cm of the seedbank ranked forth in relative sensitivity of the crucifer seedbank with low to moderate values (Table 4.2).

With a small initial seedbank the relative sensitivity of the crucifer seedbank to emergence in the first week after planting was high and the second highest of all parameters tested (Table 4.1). With large initial seedbank emergence was only the fourth most influential parameter with low relative sensitivities.

The relative sensitivity of crucifer density and biomass in potato years to emergence within the first week after planting was the third highest of the parameters studied following the seedling survival rate at hilling. The relative sensitivity of crucifer density was high for all treatment combinations, whereas the relative sensitivity of crucifer biomass was only moderate (Table 4.3). As mentioned above, the natural variability in emergence during the first week measured in the field was high. Crucifer density in the potato crop was less sensitive to emergence from the top 4 cm of the soil, with moderate to high relative sensitivities (Table 4.3). The relative sensitivity of crucifer biomass in the potato phase was moderate (Table 4.3). The difference in emergence from O-4 cm depth determined in two different years was moderate (Table 4.4).

With a small initial seedbank, crucifer plant density and biomass in potato years was highly sensitive to emergence in the first week after planting. In moldboard-plowed treatments it was the most influential factor and in chisel-plowed treatments this factor was the second most influential (Table 4.1).

With a large initial seedbank crucifer density in potato years was moderately sensitive to emergence in the first week, crucifer biomass in potato years had low sensitivity and the crucifer seedbank had very low sensitivity to this factor. Despite the moderate and low relative sensitivities of crucifer density and biomass in potato to emergence in the first week after planting, this parameter had the second highest rank in moldboard-plowed treatments and the third highest rank in chisel-plowed treatments (Table 4.1).

Table 4.4. Variability of field based parameter estimates used in the model.

Parameter	natural variability between years [a]	variability weather conditions	within treatments	between treatments or stages
seed survival O-l cm depth	57% [b]			
plant survival in potato				
hilling:				
small seedlings		wet year	0%	
medium seedlings	193%	wet year	64%	200% (between small & medium seedlings)
medium seedlings		dry year	74%	
large seedlings	138%	wet year	20%	116% (between medium & large seedlings)
large seedlings		dry year	31%	
spring-tine cultivation:				
small seedlings	57%	wet year	30%	189% (between medium & large seedlings)
small seedlings		dry year	24%	
medium seedlings	83%	dry year	31%	9 1% (between medium & large seedlings)
medium seedlings		wet year	14%	
large seedlings		wet year	12%	
emergence				
in week 1	126%			
from O-4 cm depth	42%			
in potato:				
biomass per weed	211%'	wet year	83% [d]	
biomass per weed		dry year	221% [d]	
seed production per biomass	n.d.	wet year	18%	
in rotation crops:				
biomass per weed				
barley	156%'	dry year	1445% [d]	-42% [c] (between barley and oat-pea-vetch)
barley		wet year	401% [d]	
oat-pea-vetch	135% [c]	wet year	180% [d]	14% [c] (between barley and oat-pea-vetch)
oat-pea-vetch		dry year	6500% [d]	
seed production per biomass				
barley	53% [c]	wet year	700% [d]	14% [c] (between barley and oat-pea-vetch)
barley		dry year	165% [d]	
oat-pea-vetch	178% [c]	dry year	117%"	113% [c] (between barley and oat-pea-vetch)
oat-pea-vetch		wet year	267% [d]	
seedling survival				
barley	5.4% [c]	dry year	264% [d]	13% [c] (between barley and oat-pea-vetch)
barley		wet year	300% [d]	
oat-pea-vetch	6.5% [c]	wet year	132% [d]	12% [c] (between barley and oat-pea-vetch)
oat-pea-vetch		dry year	2700% [d]	

[a] ▪ between wet and dry years
[b] ▪ between seeds produced in wet and dry years
[c] ▪ between linear conversion factors, not parameters used in nonlinear function in model
[d] ▪ for parameter c in density or biomass dependent function y = a / (1 ▪ c * x)

Jordan et al. (1995) found the germination rate to be the third most influential factor on the seedbank of Abutilon theonhrasti, as well as, Setaria viridis following seed production. The model by Lindquist et al. (1995) on the population dynamics of A. theophrasti included herbicides and two herbicide related factors, to which the economic optimum threshold was most sensitive. These factors were followed by seed survival in the soil and then emergence and seedling survival. It appears that emergence rate is generally one of the more influential factors on weed population dynamics of annual weeds.

Management practices that can influence emergence rates were not studied in context with this model. Examples for such practices are: seedbed preparation in the dark, to reduce light induced germination (Ascard, 1994); reducing the availability of NO_3^- (a germination stimulant for some weed species (Karsen and Hilhorst, 1992)) to weed seeds by nutrient management practices, such as banding of fertilizer in the row at the depth best suited for the crop and too deep for small seeded weed species (DiTomaso, 1995), timing of nitrogen fertilizer applications in order to maximize immediate N-uptake by the crop (split applications), but too late for weeds with fast initial growth rate (Alkamper et al., 1979), or by supplying N with an organic amendment that releases nitrogen slowly during mineralization (Dyck et al., 1995). Weed germination rates could also be increased in speed and numbers by applying other chemical germination stimulants, like ethephon (Mekki and Leroux, 1991). These weeds could subsequently be killed by cultivation or herbicides.

Weed survival during cultivations in the potato crop

Relative sensitivity of the crucifer seedbank density in the top 10 cm to changes in plant survival at hilling in the potato crop was the third most influential parameter with low to moderate relative sensitivities; sensitivity of the seedbank from O-20 cm was low (Table 4.2). Differences between wet and dry seasons in the survival rates of crucifers for hilling were large for medium and large seedlings (Table 4.4). The high natural variability, found for this parameter, might make it just as important as emergence from 0 to 4 cm depth for which much lower natural variability was measured (Table 4.4).

With a small initial seedbank, crucifer survival of hilling ranked fourth in relative sensitivity of the crucifer seedbank, with a large initial seedbank, this parameter ranked last of the parameters tested together with emergence during the first week after planting (Table 4.1).

Survival of spring-tine cultivations was less influential, but the relative sensitivity of the seedbank from O-10 cm depth was still moderate (Table 4.2). The simulations used for sensitivity analysis contained only one pass with a spring-tine harrow preemergence to potato; increasing the number of cultivations might increase the importance of these parameters. Sensitivity analysis on parameters for mechanical weed control in growing crops have not been published elsewhere to date.

Plant survival at hilling in the potato crop was the most influential factor for crucifer density and biomass in potato in moldboard-plowed treatments and second most influential in chisel-plowed treatments with high relative sensitivity for crucifer density and moderate relative sensitivity for crucifer biomass (Table 4.3).

With a large initial seedbank, crucifer density and biomass in potato years were most sensitive to seedling survival at hilling. With a small initial seedbank crucifer density and biomass in potato had the third highest relative sensitivity to plant survival at hilling (Table 4.1).

The difference between wet and dry seasons in the survival rates of crucifers for hilling was high (Table 4.4). For hilling the difference between small and medium crucifer seedlings in wet years was very large, between medium and large seedlings the difference was not as great, but still large (Table 4.4); consequently, delaying hilling until crucifer seedlings are larger, would result in a considerable reduction in the success of weed control.

Crucifer survival of spring-tine cultivation was the fifth most influential factor following emergence rates from the top 4 cm of the soil. The relative sensitivity of crucifer density in potato years was moderate and of crucifer biomass low to moderate (Table 4.3). The difference in survival rates of spring-tine cultivation of small and medium crucifer seedlings between dry and wet years was greater than for emergence rates from the top 4 cm (Table 4.4). Delayed cultivation would substantially increase survival rates, as the differences in survival rates between medium and large seedlings for spring-tine harrowing were large (Table 4.4). Treatment effects on emergence from the top of the soil seed bank were not studied.

Seed production per unit of biomass in potato

Seed production per unit of biomass in potato years was the second most influential parameter on the seedbank of the crucifer complex with moderate relative

sensitivities of the upper seedbank (O-10 cm depth) (Table 4.2) and slightly lower but also moderate sensitivity of the total seedbank from O-20 cm depth (Table 4.2). Chisel-plowed treatment simulations had higher relative sensitivities than moldboard-plowed treatment simulations for both depth intervals. Seed production per unit of biomass was only studied in one year (Chapter 3), thus differences between different seasons could not be calculated.

Relative sensitivity of crucifer plant density and biomass in potato was generally low to seed production per unit of biomass, however, crucifer density was somewhat more sensitive than crucifer biomass (Table 4.3). If seed production per unit of biomass was much higher in years with weather conditions different from the only year in which it was measured, this factor would be of greater importance. Large differences in the fecundity of Lolium rigidum Gaud. (Fernandez-Quintanilla et al., 2000) and Avena sterilis (Fernandez-Quintanilla et al., 1986) were found between different years and different sites.

Seed production was the second most influential factor on the seedbank for A. theonhrasti and S. viridis in the model by Jordan et al. (1995). In that study, the values for relative sensitivity for A. theophrasti, the species with long-lived seeds, were in the same range as the relative sensitivity of the seedbank from O-10 cm to seed production per unit of biomass in potato in our model. Lindquist et al. (1995) found maximum seed production per plant to be the fourth most influential parameter, of the parameters not related to herbicide use, on economic optimum threshold density of A. theonhrasti.

Density or biomass dependent parameters

All state variables studied had low relative sensitivities to the density- and biomass-dependent parameters in the functions for crucifer plant survival in rotation crops, biomass per plant in both the rotation crop and potato years of the simulations, and seed production per unit of biomass in rotation crop years. The only exception to this is the relative sensitivity of the crucifer density in potato years in the simulation with chisel-plowing and barley as rotation crop is 0.55 which is just in the moderate range, however, its rank is still only sixth (Table 4.2 and 4.3). Thus it appears that the model in general is fairly robust to the parameters for density- and biomass-dependence, therefore the large standard errors associated with these parameters (Table 4.4; Chapter 3) are not as much of a concern.

Even though the relative sensitivity of all state variables tested to crucifer survival in the rotation crops, as well as, differences between the rotation crops and between years within each rotation crop in this parameter were small (Tables 4.1, 4.2 and 4.3), management practices, like spring-tine harrowing or reduced rates of herbicides in the rotation crops, could result in a reduction of the crucifer population, if they result in strongly increased seedling mortality compared to the natural mortality.

Simulations with Large and Small Initial Seedbanks

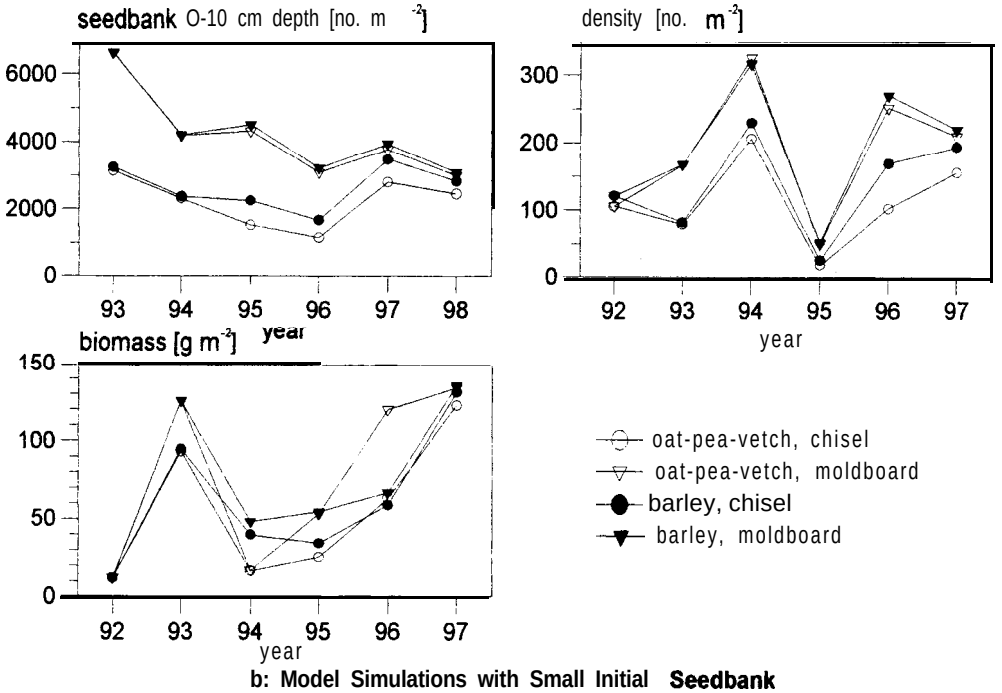
The simulations with a large initial seedbank overall exhibited a decreasing trend for the seedbank from O-l 0 cm depth. Even though the seedbank increased due to high

seed input in the wet 1996 season, the average size of the seedbank from O-10 cm was around 3000 m^{-2} in spring 1998, i.e. it was about half of the initial seedbank in 1992 (Fig. 4.1). In contrast, the simulations with a small initial seedbank had an overall increasing trend for the seedbank from O-10 cm. With a small initial seedbank there were considerable differences in the size of the simulated seedbank depending on the rotation and tillage treatment combination (Fig. 4.1). For spring 1998 the seedbank density ranged from between 50 and 100 viable seeds m^{-2} to just under 800 m^{-2}.

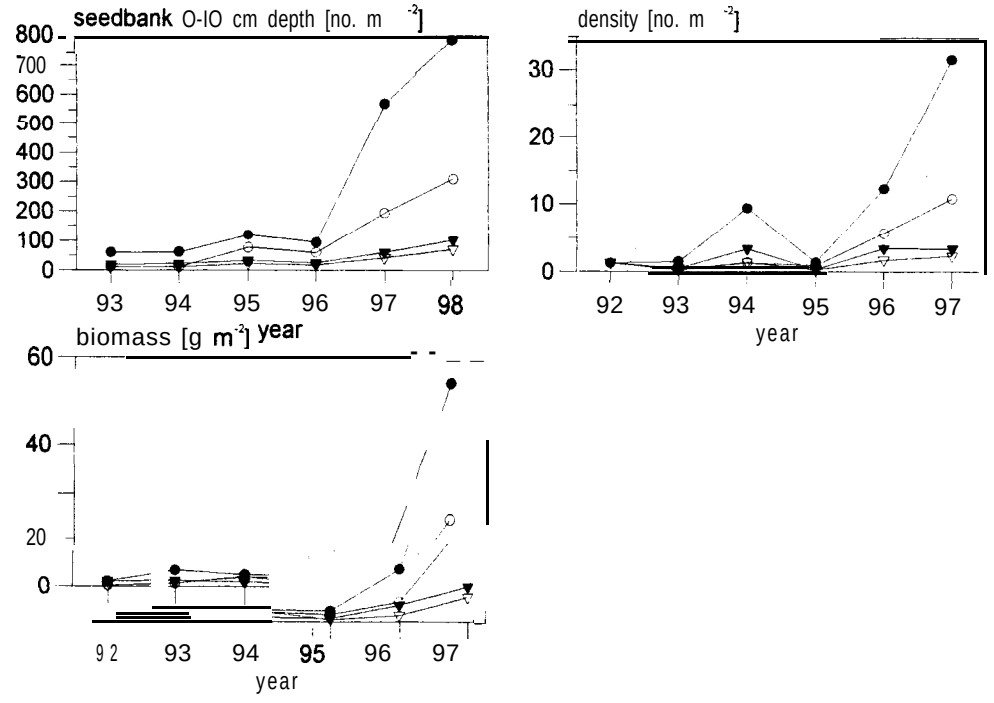
Large initial seedbank simulations with moldboard-plowing resulted consistently in higher seedbank predictions than chisel-plowing until year six (Fig. 4.1). The small initial seedbank simulation results were lower for moldboard than for chisel-plowed treatments (Fig. 4.1). These findings can be explained as follows: A field with a large initial seedbank is a field with a history of high weed seed input. A change in management practices that results in reduced weed infestation also results in reduced seed density near the soil surface. Seed loss due to germination and mortality is not fully compensated by the amount of new seed produced. If this field is moldboard-plowed, soil from lower horizons that contains higher weed seed densities than the surface soil is brought to the soil surface. In contrast, with a small initial seedbank the same management practices can result in new weed seed input that exceeds the loss from the surface seedbank. Because the soil lower in the soil profile still contains very low weed seed densities, moldboard-plowing brings to the surface soil containing very few seeds resulting in a lower weed infestation than chisel-plowing which leaves the more numerous freshly produced seeds near the soil surface. These findings are in agreement

Figure 4.1. Simulations with large and small initial seedbanks.
(a) Model simulations with large initial seedbank of 6000 seeds m^{-2} from O-10 cm depth in the soil. **(b)** Model simulations with small initial seedbank of 10 seeds m^{-2} from O-10 cm depth in the soil.
Primary tillage was simulated prior to planting the potato crop in odd numbered years.

a: Model Simulations with Large Initial **Seedbank**



b: Model Simulations with Small Initial **Seedbank**



with Mohler's (1993) model on the influence of tillage practices on weed populations and a field study by Schweizer and Zimdahl(l984).

With a large initial seedbank, the seedbank from O-10 cm depth was consistently greater in rotations with barley than with oat-pea-vetch within each of the tillage systems. The difference between rotation crops was greater in chisel- than in moldboard-plowed treatments. Crucifer density was also consistently greater in rotation with barley than with oat-pea-vetch in chisel-plowed treatments. In moldboard-plowed treatments no consistent difference could be observed (Fig. 4.1). With a small initial seedbank, the simulation results were consistently greater in rotation with barley than oat-pea-vetch within each of the tillage systems for all state variables, crucifer seedbank, density and biomass (Fig. 4.1).

In the field study used for validation (Chapter 2) differences between crucifer populations in the two rotation crops were less consistent. This was probably at least partly due to the fact that the initial seedbank at the start of the six year study happened to be greater in plots planted with oat-pea-vetch than in plots planted with barley. Relative to the size of the initial seedbank the seedbank in rotations with barley increased more than in rotations with oat-pea-vetch (Chapter 2). In spite of this, crucifer biomass was consistently greater in barley than in oat-pea-vetch (statistically significant in only two of the three years) and crucifer density was greater in barley in two (significant only in one year) out of three years in the rotation crop phase.

Weather Simulations

Overall, simulations containing years that were wet throughout the entire growing season resulted in populations higher in all state variables than simulations of other weather conditions. The second largest predicted crucifer populations occurred in simulations that contained three wet and three dry years (Fig. 4.2 and 4.3). Simulations with three wet years followed by three dry years had higher crucifer populations than three dry years followed by three wet years (Fig. 4.2 and 4.3). At the end of the simulation period this ranking was reversed for chisel-plowed treatments (Fig. 4.2 and 4.3).

Simulations that did not contain any wet seasons resulted in smaller crucifer populations than any of the simulations containing wet seasons (Fig. 4.2 and 4.3). Simulations with early-dry/late-wet seasons in all years consistently resulted in the largest population within this group; simulation with all years dry resulted in the smallest population (Fig. 4.2 and 4.3).

These predictions match the expectation that the crucifer populations would be larger when more wet weather conditions were included in the simulation, because the crucifers produced more biomass and consequently seeds in wet than in dry years in the field studies used to obtain the model parameters (Chapter 3).

Different annual weather patterns resulted in large differences in simulated crucifer populations. Different weather conditions also resulted in changes of the ranking of crucifer infestations among the treatment combinations of tillage practice and rotation crop (Fig. 4.2 and 4.3).

Figure 4.2. Simulations with different weather conditions.
for two-year potato - oat-pea-vetch rotations. --- Moldboard-plowed simulations, ——— chisel-plowed simulations. Only potato years are depicted.

Weather simulations on potatoes in rotation with oat-pea-vetch

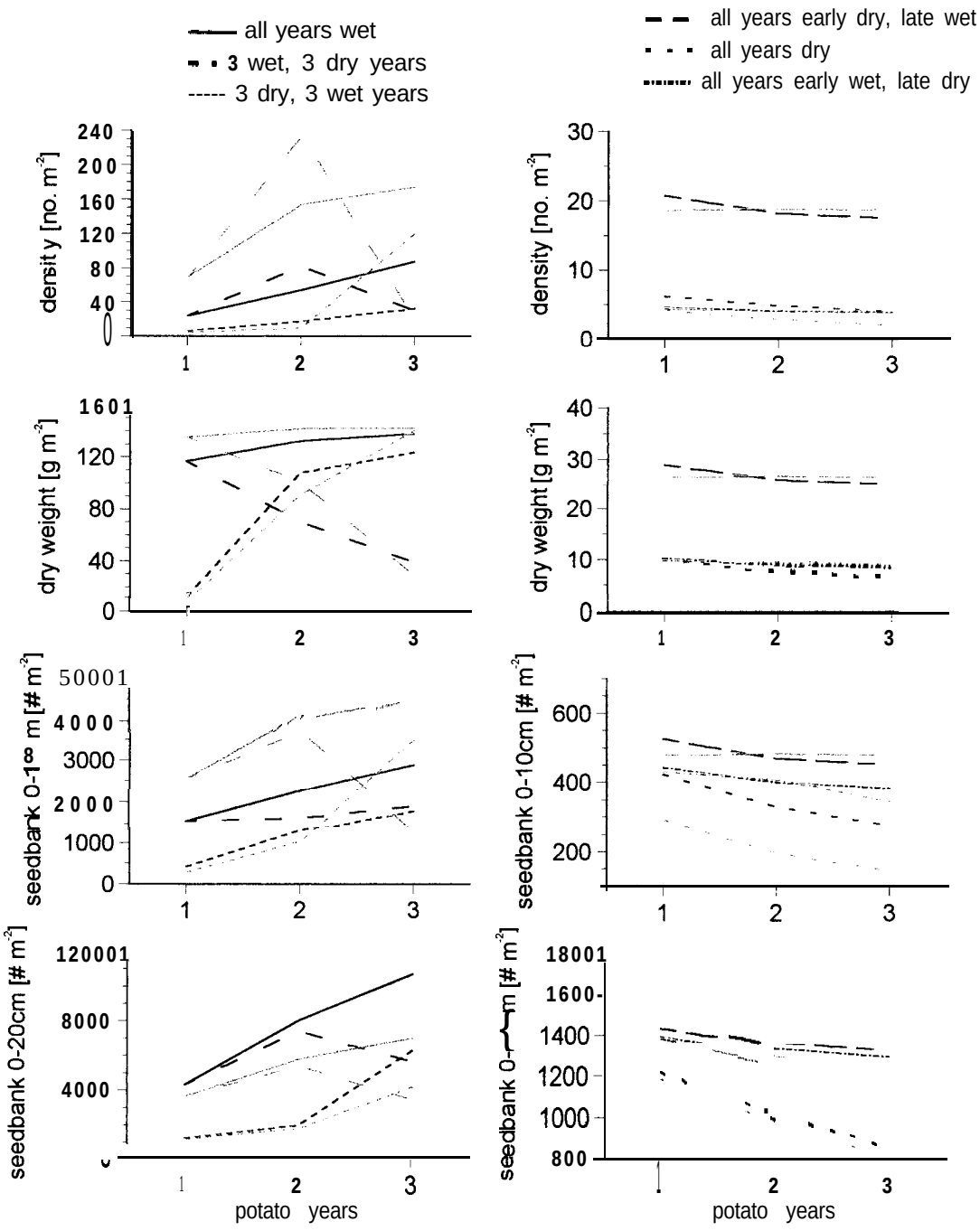
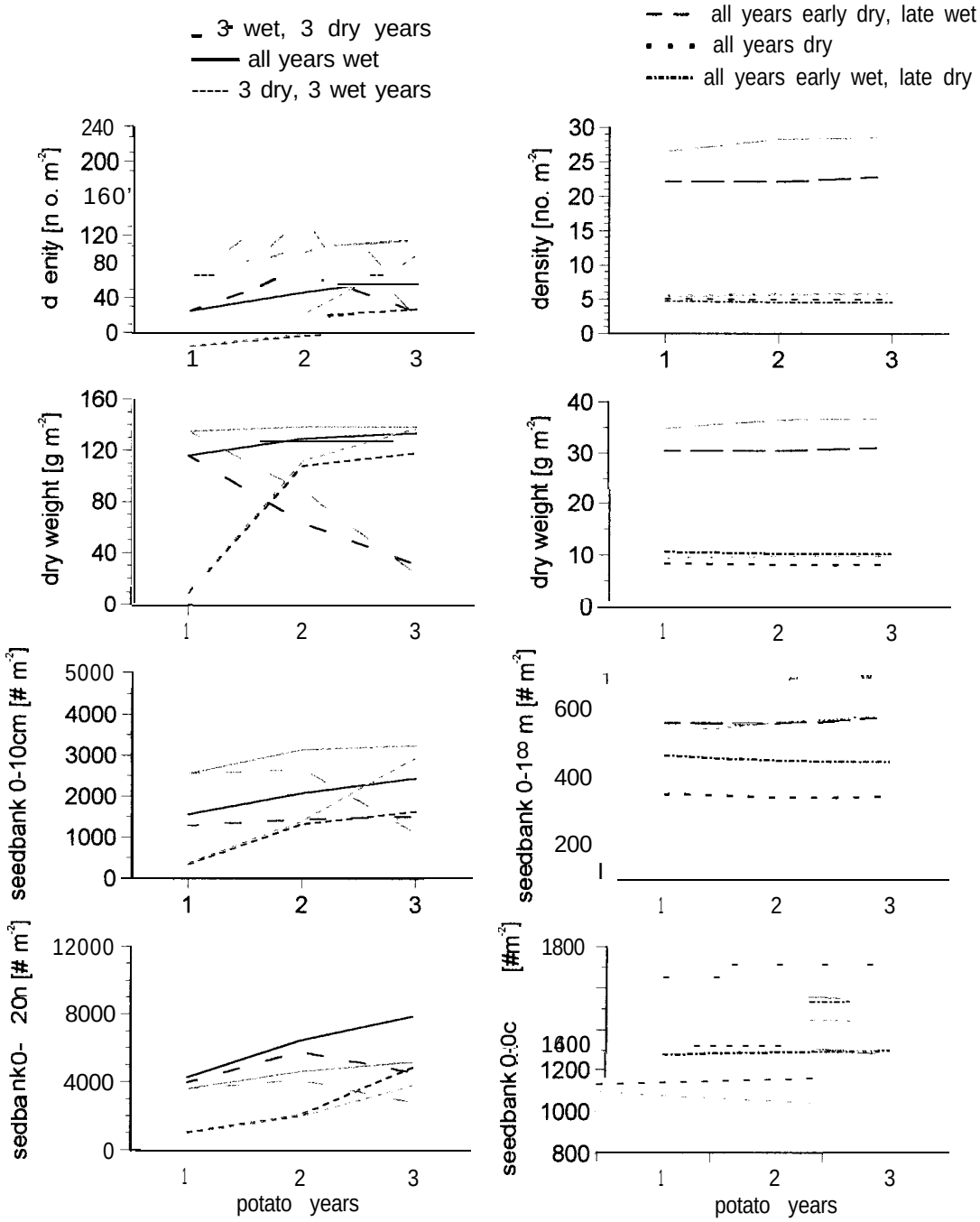


Figure 4.3. Simulations with different weather conditions for two-year potato - barley rotations. ——— Moldboard-plowed simulations, ... chisel-plowed simulations. Only potato years are depicted.

Weather simulations on potatoes in rotation with barley



In simulations with all years wet, predicted crucifer density, biomass and seedbank from O-10 cm depth were consistently higher in chisel than in moldboard-plowed treatments. Whereas the predicted seedbank from O-20 cm depth was higher in moldboard than in chisel-plowed treatments (Fig. 4.2 and 4.3). This result was expected, because the crucifers produce more seeds in wet years than in years with other weather conditions (Chapter 3). In chisel-plowed treatments these numerous freshly produced seeds stay near the soil surface where they can germinate and contribute strongly to the next generation. In contrast, in moldboard-plowed treatments, the freshly produced seeds are moved to deeper soil horizons where they cannot germinate successfully and therefore contribute less to the following generation (Mohler, 1993).

In simulations with all years dry, moldboard-plowed treatments have higher crucifer density, biomass and seedbank than chisel-plowed treatments in rotation with oat-pea-vetch. Because crucifers produce only very few seeds in oat-pea-vetch in dry years (Chapter 3), this result was expected. Due to the small seed input and higher loss of seeds from shallow depths due to germination and mortality there is a lower density of seeds near the soil surface than in deeper soil horizons. If chisel-plowing is performed in this situation fewer seeds are in a position where they can germinate successfully than if moldboard-plowing is performed bringing up more numerous seeds from deeper soil horizons.

In simulations with three wet years followed by three dry years crucifer biomass in the wet potato year and the first dry potato year that directly followed the three wet years was higher in chisel than in moldboard-plowed treatments, in contrast in the last potato year (dry) crucifer biomass was lower in chisel than in moldboard-plowed

treatments. The upper seedbank from O-10 cm depth from which crucifer seeds can germinate (Chapter 3) had higher densities for moldboard than for chisel-plowed treatments, only when three wet years were followed by three dry years in the simulation. These results were expected, because there was less seed input in the dry years resulting in lower seed densities in the upper soil in chisel-plowed treatments. In contrast, moldboard-plowing brings up soil containing higher seed densities originating from seed shed in the wet years in the beginning of the simulation and therefore results in higher crucifer populations than chisel-plowing.

There were strong contrasts in the predicted crucifer populations for the different tillage treatments depending on the weather conditions simulated. However, because the difference in growth and seed production of the crucifers between wet and dry years is known from field studies (Chapter 2), all the simulated tillage effects were as expected from an analytical model by Mohler (1993) and several field studies (Schweizer and Zimdahl, 1984; Burnside et al., 1986; Chapter 2).

In simulations with all years wet, crucifer plant and seed density were greater and crucifer biomass was slightly greater in rotation with oat-pea-vetch than with barley (Fig. 4.2 and 4.3). At the end of any of the simulations containing wet years treatments in rotation with oat-pea-vetch had higher seedbanks than treatments in rotation with barley, whereas in the simulations not containing wet years the ranking of the seedbank density was reversed. This simulation result that predicted crucifer populations were larger in rotation with oat-pea-vetch than with barley was not expected. In the field study used for validation of this model, oat-pea-vetch was more suppressive towards crucifers than

barley in most years, however, this difference was not consistently statistically significant (Chapter 2). Closer study of the parameters used in the model revealed that the only explanation for this simulation result is a stronger density-dependent effect in barley than in oat-pea-vetch on plant survival to maturity and biomass per plant in wet years. Due to the proportionally large standard errors in the parameters for density-dependence (Table 4.2) it appears questionable, whether this model prediction is realistic.

The predicted crucifer populations were smaller in oat-pea-vetch than in barley in simulations with all years dry. This result is consistent with expectations, because biomass per plant in dry years was much greater in barley than in oat-pea-vetch (Chapter 3).

The relative size of the predicted crucifer populations for the two rotation crops varies with the simulated weather conditions.

Several other studies found direct, as well as, indirect effects of weather on weed populations. Setaria viridis emergence and growth appeared to be enhanced by higher rainfall (McGiffen et al., 1997), however, S. viridis biomass was reduced by higher rainfall probably due to higher competitiveness of the corn and soybean crops in years with more moisture. Buhler (1999) also found effects of mechanical and chemical weed control treatments on weed populations to vary between years in corn-soybean rotations. He concluded that different environmental conditions affected the efficacy of the weed control treatments used. Sheley and Larson (1994) found that Centaurea solstitialis (yellow star-thistle) seed production per unit area in rangeland was strongly reduced in a dry year compared to a wet year even though the density was the same in both years.

Simulations with contrasting weather conditions have drastically different outcomes (Fig. 4.2 and 4.3). This indicates that a field study performed in years with different weather conditions could have quite different outcomes in terms of population size and differences between treatments. If global warming, as has been predicted, results in more extreme weather conditions, more extremely dry and/or extremely wet seasons are likely to occur. These model simulations indicate that such climate changes could have profound effects on weed populations.

The results of the weather simulations stress the importance of weather for weed population dynamics and demonstrate that the inclusion of weather in weed population dynamics models is crucial in climates with variable weather conditions from year-to-year. It also indicates that a weed population dynamics model will most likely not result in accurate predictions in an area with different climatic conditions. For purely demographic models new parameters will have to be obtained to account for the local weather conditions and biotypes of the weeds, a model containing mechanistic physiological processes might not need new parameters, but should be validated in the new conditions.

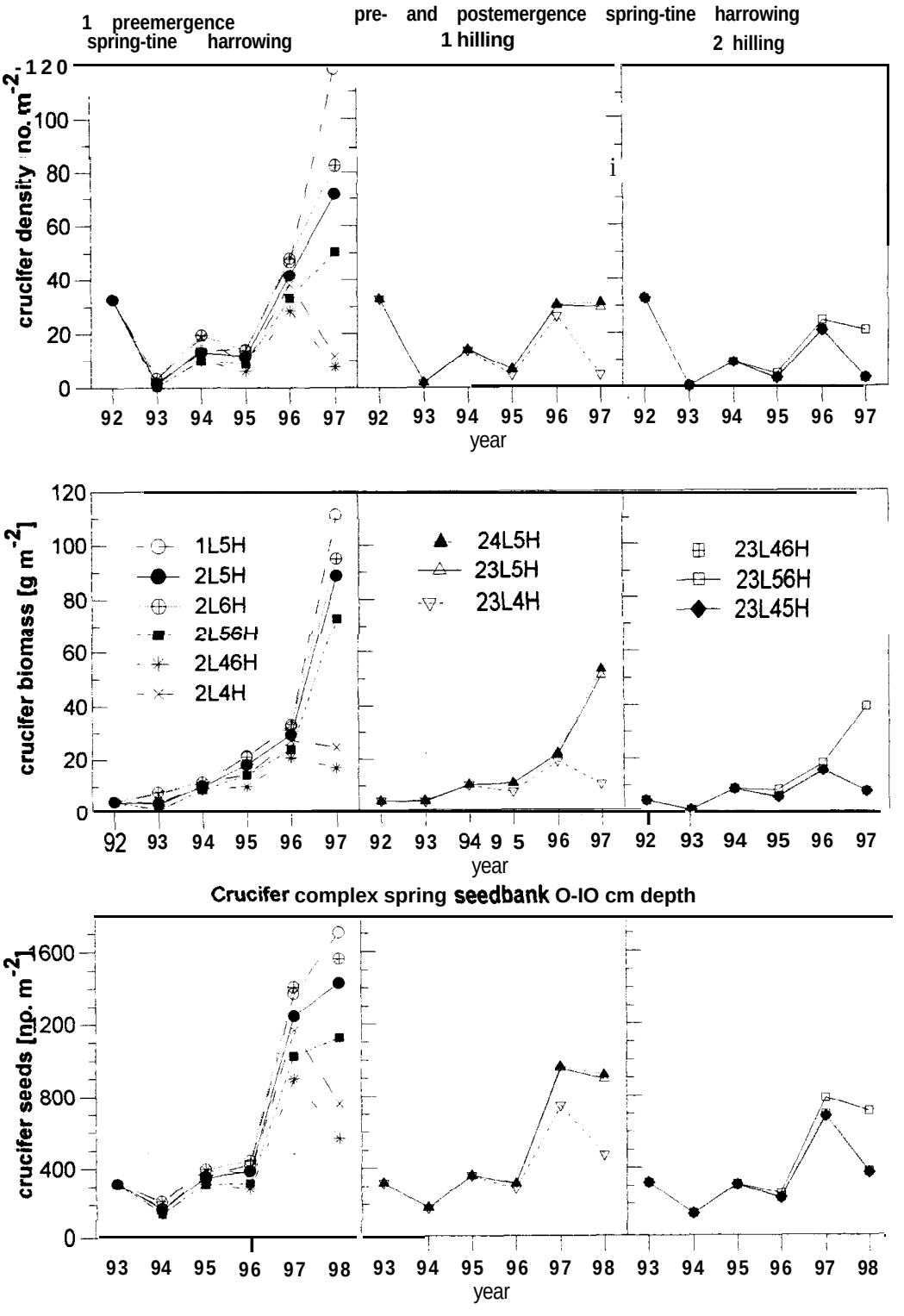
Simulations with More Cultivations in Potato Years

Crucifer complex population density measured as density of mature plants in the field, as soil seedbank from O-10 cm and from O-20 cm depth, as well as biomass of mature crucifer plants in the field was lowest when potato hilling was done earlier (4 WAP < 5 WAP < 6 WAP). A second hilling reduced the crucifer population compared to

one hilling when the single hilling was done at the same time as the first hilling in the simulation with two hillings (Fig. 4.4). Preemergence spring-tine harrowing resulted in lower crucifer populations when simulated 2 WAP than 1 WAP. However, this result might not be very realistic, because the data used to obtain the survival parameters during cultivations don't contain any information about germinated weeds that have not yet emerged and the effect of cultivation on these seedlings. Adding postemergence spring-tine harrowing to the preemergence harrowing reduced the crucifer populations more when done earlier (3 WAP) than when done later (4 WAP) (Fig. 4.4). Of all cultivation treatments simulated, the combination of spring-tine harrowing 2 and 3 WAP and hilling 4 and 5 WAP resulted in the lowest crucifer populations. This best treatment was followed by spring-tine harrowing 2 and 3 WAP and hilling 4 and 6 WAP, and spring-tine harrowing 2 and 3 WAP and hilling 4 WAP only. Even these best treatments have an increasing trend in the crucifer seedbank following potato years within the six year simulation period. This result suggests that additional management practices need to be included to prevent the crucifer population from increasing.

The results of these model simulations are corroborated by a number of studies that found earlier cultivations to result in better weed control than later cultivations of the same intensity (e.g.: Böhrnsen and Brautigam, 1990; Rydberg, 1995). However, if the crop can withstand more intense cultivation later in its development than when it is very small, delayed spring-tine harrowing has been shown to increase selectivity between crop and weeds (Rasmussen, 1992; Rasmussen, 1991). Potato can withstand the most intense spring-tine harrowing preemergence. Post-emergence spring-tine harrowing has to be less intense to avoid crop damage. Larger post-emergence potato plants cannot withstand

Figure 4.4. Simulations with various cultivation regimes in potato years in chisel-plowed oat-pea-vetch - potato rotations. L - sprmg-tine harrowing; H - hilling; 1, 2, 3, 4, 5, and 6 represent the number of weeks after planting for each cultivation simulated.


1 preemergence spring-tine harrowing
pre- and postemergence spring-tine harrowing
1 hilling
2 hilling
crucifer density no. m-2
120
100
80
60
40
20
0
92 93 94 95 96 97 92 93 94 95 96 97 92 93 94 95 96 97
year
crucifer biomass [g m-2]
1L5H
2L5H
2L6H
2L56H
2L46H
2L4H
24L5H
23L5H
23L4H
23L46H
23L56H
23L45H
92 93 94 95 96 97 92 93 94 9 5 96 97 92 93 94 95 96 97
year
Crucifer complex spring seedbank O-IO cm depth
crucifer seeds [no. m-2]
1600
1200
800
400
0
93 94 95 96 97 98 93 94 95 96 97 98 93 94 95 96 97 98
year

more intense spring-tine harrowing than smaller plants, so earlier spring-tine harrowing results in greater weed control because the intensity cannot be increased when the spring-tine harrowing is performed later.

Summary and Conclusions

The general simulation trend of the crucifer population dynamics measured as relative sensitivity of the crucifer seedbank was highly sensitive only to seed survival in the top centimeter in the soil. The seedbank was much less sensitive to all other parameters tested. For the seedbank from O-l 0 cm and from O-20 cm depth, weed survival at hilling, seedling emergence in week 1 and seed production per unit of biomass in potato years were the next most influential parameters. Their relative sensitivities were quite low, however, ranging from 0.33 to 0.74. All other parameters analyzed had even lower relative sensitivities. Overall the upper seedbank from O-10 cm depth was slightly more sensitive to changes in parameters than the total seedbank from O-20 cm depth. Chisel-plowed treatments had higher relative sensitivities than moldboard-plowed treatments. Crucifer density was more sensitive to changes in the parameters than crucifer biomass. Crucifer populations with a small initial seedbank were much more sensitive to changes in parameters than crucifer populations with large initial seedbanks, but for the most part the order of importance of the parameters tested remained the same for all initial seedbank densities used (Tables 4.1, 4.2 and 4.3). These findings suggest that further research on the processes affecting seed survival in the soil and management practices that can increase the mortality of seeds in the soil is of particular importance.

In simulations with a small initial seedbank, crucifer populations increased in all treatments, but they increased more in chisel-plowed than in moldboard-plowed treatments. In simulations with a large initial seedbank the crucifer population decreased in all treatments, with higher seedbank predictions for moldboard- than for chisel-plowed treatments. This indicates that the simulated crucifer populations would not continue to increase indefinitely in long-term simulations that go beyond the 20 years simulated (Chapter 3).

Simulations containing wet years resulted in larger simulated crucifer populations than simulations not containing wet years. Simulations containing only dry years resulted in the smallest crucifer populations. Overall, simulations with different weather conditions resulted in large differences in the size of the predicted crucifer populations, as well as, in changes in the ranking of the size of predicted crucifer population state variables between different treatments, indicating the importance of including weather conditions in weed population dynamics models.

Increasing the number of spring-tine cultivations, as well as, hillings in the potato crop and optimizing the timing of these cultivations reduced the simulated crucifer population considerably. Hilling reduced crucifer populations more when it was done earlier (4 WAP) than when it was done later (5 or 6 WAP), and a second hilling following an early first hilling improved the reduction of the crucifer population. Preemergence spring-tine harrowing was more effective 2 WAP than 1 WAP. Postemergence spring-tine harrowing was more effective when done earlier (3 WAP rather than 4 WAP). However, even the best cultivation treatments simulated could not completely prevent an increase in the total spring seedbank in years following potato

years, indicating that additional weed management practices need to be studied and incorporated in the crop management system to prevent an increase in the crucifer population.

Numerous other approaches can be taken to reduce weed populations that have not been discussed here. One approach that could be particularly effective in potato rotations in northern Maine is the inclusion of perennial forage crops in the rotation. This would interrupt the life-cycle of the dominant annual spring weeds, and would introduce mowing or grazing into the cropping system to prevent weed seed production. In order to test this approach with the model more experiments would need to be conducted to obtain parameters, such as crucifer emergence in a growing forage crop, crucifer survival, biomass and seed production in the forage crop and the influence of different times and intensities of mowing and grazing on these parameters.

5. SUMMARY AND CONCLUSIONS

Summary of Results

In the six year field study the oat-pea-vetch green-manure mixture showed consistent superior weed-suppressive ability towards Chenopodium album, Gnanhalium uliginosum, and all other weed species with the exception of a complex of cruciferous weed species. The biomass of the 'crucifer complex' was only significantly reduced in oat-pea-vetch compared to barley in two out of three rotation crop years, and the density only in one out of three years. The population of the 'crucifer complex' increased over the period of the study, while the population of C. album decreased. The results of this study do not support the hypothesis that this shift in weed species composition was due to a competitive effect of the weeds of the 'crucifer complex' on C. album. No rotation crop effects on weeds growing in potato years could be detected. However, the germinable spring seedbank of G. uliginosum was smaller in rotation with oat-pea-vetch than with barley in all years from 1993 through 1997. In 1992 and 1994 weed species richness was greater in barley than in the more competitive mixture of oat, pea and hairy vetch. In 1995 this effect carried through into the potato year. Weed species evenness was greater in oat-pea-vetch than in barley in 1992. In contrast, in the potato year, 1995, weed species evenness was significantly greater following barley than following oat-pea-vetch. Since weed density tends to be correlated with weed density and seed production in the previous year, the rotation crop effect on weed species evenness is not conclusive.

Tillage effects were only observed for the 'crucifer complex'. The germinable spring seedbank of the 'crucifer complex' in 1997, as well as, the crucifer plant density in 1995 and 1997 were significantly larger in chisel-plowed than in moldboard-plowed plots. The population of the 'crucifer complex' increased significantly faster with chisel-plowing than with moldboard-plowing, because the larger seed input of the most recent year stayed near the soil surface where the seeds could germinate successfully when chisel-plowed, whereas moldboard-plowing would bury the freshly shed large seed population too deeply for successful germination and bring up seeds produced in earlier years in which the crucifer population was still smaller and fewer seeds were produced.

In potato years total weed density and C. album density declined over the course of the study while the density of the 'crucifer complex' increased. Total weed biomass in 1997 (78.1 g m^{-2}) was much higher than in 1993 (21.6 g m^{-2}) and 1995 (14.6 g m^{-2}). This increase was due to an increase in the biomass of the 'crucifer complex' and low potato seed piece quality. In 1993 and 1995, US #1 yield was comparable to average commercial yields in northern Maine and was not significantly reduced by the presence of weeds. In 1997, US #1 yields in the experiment were lower than on commercial fields in the area due to poor seed piece quality. This was also the only year in which a statistically significant yield reduction due to weeds (29%) was detected, This reduction probably resulted from increased interference by the 'crucifer complex' in combination with reduced potato competitiveness due to poor seed piece quality.

Validation showed that the simulation model of the population dynamics of the 'crucifer complex' performed better when density-dependent functions and weather

conditions were included in the model. Twenty-year simulations, using historical weather records for Presque Isle, ME from 1968 to 1997, and the mean initial germinable seedbank from the field study used for validation (339 seeds m^{-2} from O-10 cm depth) predicted no consistent differences between the rotation crop treatments (oat-pea-vetch vs. barley) and the tillage treatments (chisel- vs. moldboard-plowing). The variation between years was greater than the differences between treatments in the results of the 20-year simulations, demonstrating importance of weather conditions for crucifer population dynamics. The seedbank of the 'crucifer complex' was still increasing at the end of the 20-year simulations. But simulations with a large initial seedbank (6000 seeds m^{-2} from O-l 0 cm depth) resulted in a considerable decrease in the size of the crucifer population over the course of a six-year simulation.

Sensitivity analysis indicated that the seedbank of the 'crucifer complex' was particularly sensitive to changes in seed survival near the soil surface, followed by seed production per unit biomass in potato years, seedling survival at hilling, and seedling emergence during the first week after planting (WAP). Crucifer plant density and biomass in potato years were particularly sensitive to changes in seed survival near the soil surface and seedling survival at hilling, followed by seedling emergence in the first WAP and seedling emergence from the top 4 cm of the soil. Ranking of the sensitivity to the parameters changed little when the simulations were started with a small initial seedbank (10 seeds m^{-2} from O-l 0 cm depth) or a large initial seedbank (6000 seeds m^{-2} from O-10 cm depth). The values of the relative sensitivities, however, where much larger in simulations with a small initial seedbank than in simulations with a large initial seedbank.

Simulations with contrasting weather conditions resulted in considerable differences in the size of the predicted crucifer populations. Overall simulated wet years resulted in much higher predicted crucifer populations than early-dry/late-wet, early-wet/late-dry and dry years. Chisel-plowing resulted in greater predicted crucifer populations than moldboard-plowing when it followed wet years, whereas this relationship was reversed when the tillage practices followed dry years. In simulations containing wet years, oat-pea-vetch as rotation crop resulted in larger predicted crucifer populations than barley as rotation crop. In simulations not containing wet years this relationship was reversed.

Simulations with various cultivation regimes in potato years indicated that crucifer populations can be strongly reduced by hilling earlier rather than later. Adding a second hilling further reduced the crucifer population. Spring-tine harrowing prior to potato emergence resulted in greater reduction in crucifer density when it was performed 2 WAP than 1 WAP. Spring-tine harrowing after potato emergence was more effective when performed 3 WAP than 4 WAP. The lowest crucifer populations were predicted with the combination of spring-tine harrowing 2 and 3 WAP and hilling 4 and 5 WAP.

Recommendations for Future Research

Oat-pea-vetch was more weed-suppressive than barley but not sufficiently effective at suppressing the 'crucifer complex'. In addition, the seeds for this green-manure mixture are expensive and there is no revenue from this crop. Consequently it is not economically viable. Further research should therefore focus on studying the effects

of alternative rotation crops on weed population dynamics and in particular the crucifer complex in potato-based rotations. Promising candidates for such rotation crops are forages which give farmers a return. These forage crops should be highly competitive crops or crop mixtures that introduce additional selection pressures against weeds into the cropping system like mowing or grazing and a change in planting time. The options for climates with short seasons are mostly perennial crops like alfalfa or hay mixtures that may contain alfalfa or warm season crops like sorghum-sudan grass or Japanese millet.

Future research should focus on improving the understanding of processes identified as particularly influential on crucifer population dynamics in sensitivity analysis. Seed survival in the soil, has received some research efforts, but to date the understanding of the processes involved is still limited. Research on this process should try to avoid artificially excluding some of the mortality causing agents unless it is part of a deliberate exclusion experiment. Management practices that are likely to influence seed survival in the soil should also receive more research. Since freshly produced seeds initially lie on the soil surface and seed mortality on the soil surface tends to be particularly high one possible approach are experiments with different times between weed seed production and tillage should be studied. This could be combined in a factorial experiment with different types and amounts of crop residues left in the field that are likely to affect the activity of seed predators.

Another process that was identified as influential on crucifer population dynamics by sensitivity analysis is crucifer seed production per unit biomass in potato. One

approach to reduce this parameter could be the selection and breeding of more weed-suppressive potato cultivars. Crucifer seedling emergence in first week after planting was also identified as influential. Future research should focus on methods that might delay the time of crucifer emergence relative to the time of crop emergence. In potato one method that should be studied is mulching which might delay crucifer emergence due to physical and chemical changes in the soil environment. Placement, timing and source of nitrogen applied in the rotation crop phase could also affect relative time of emergence between the crucifers and the crops, because nitrate has been found to be a germination stimulant for many weed species.

Further research on cultivations is also important, in particular on the effect of spring-tine harrowing on weeds that have germinated but not emerged yet and on the effects of spring-tine harrowing on weed seedling mortality in drilled crops grown in rotation with potato. Crucifer survival in rotation crops was not identified as particularly influential in sensitivity analysis, but it could be more influential if it was decreased strongly by cultivation.

Conclusions

None of the management practices studied in the field experiment could prevent the population of the 'crucifer complex' from increasing to damaging levels. Oat-pea-vetch and moldboard-plowing did not suppress the crucifers sufficiently to halt the population increase. In model simulations it appeared that optimal timing of spring-tine harrowing and hilling each performed twice in potato years could strongly reduce if not

halt the increase of the crucifer population. However, optimal timing of cultivations in the field is often prevented by adverse weather conditions thus pure reliance on cultivations for weed control will not result in satisfactory weed management in all years. Consequently no one management practice alone can keep the weed populations reliably below damaging levels. That means that in order to replace the use of herbicides for weed control an approach that integrates multiple management practices to reach the goal of keeping weed populations below damaging levels needs to be taken. Such a multifaceted approach to weed management has the added advantage that it applies many different types of selection pressure to weed populations which is unlikely to result in selection for resistant biotypes or one dominant weed species that is particularly well adapted. When designing such crop management systems, the researcher should always keep in mind that the system must be economically viable in order to be adopted by farmers.

Weather was found to be very influential on the weed population dynamics in the field and the inclusion of weather conditions in the population dynamics simulation model for the 'crucifer complex' improved model performance. In simulations with the model, weather conditions resulted in large differences in the size of the population, as well as, in the relative outcome between treatments. Consequently, future weed population dynamics models for climatic regions with variable weather conditions should include weather in order to show more realistic behavior. The results also show that weed population dynamics models cannot be used to reliably predict the behavior of a weed population in any particular year beforehand, since the weather conditions that will occur during the season are not known yet.

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APPENDIX A: MATRICES USED IN MODEL

p(t) = population vector:

$$\mathbf{p}(t) = \begin{vmatrix} \text{mature weeds or weed biomass} \\ \text{large seedlings} \\ \text{medium seedlings} \\ \text{small seedlings} \\ \text{seeds O-l cm depth} \\ \text{seeds 1-2 cm depth} \\ \text{seeds 2-4 cm depth} \\ \text{seeds 4-6 cm depth} \\ \text{seeds 6- 10 cm depth} \\ \text{seeds 10- 15 cm depth} \\ \text{seeds 15-20 cm depth} \end{vmatrix} = \begin{vmatrix} p_1(t) \\ p_2(t) \\ p_3(t) \\ p_4(t) \\ p_5(t) \\ p_6(t) \\ p_7(t) \\ p_8(t) \\ p_9(t) \\ p_{10}(t) \\ PI_1(t) \end{vmatrix}$$

t = at time t any time during the course of the simulation

$\mathbf{G}_w$ = germination, seedling survival and development matrices at w weeks after planting:

$$\mathbf{G}_w = \begin{vmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 11, & \text{m l}, & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & mm_w & sm_w & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & ss_w & g_{5w} & g_{6w} & g_{7w} & g_{8w} & g_{9w} & g_{10w} & g_{11w} \\ 0 & 0 & 0 & 0 & mg_{5w} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & mg_{6w} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & mg_{7w} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & mg_{8w} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & mg_{9w} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & mg_{10w} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & mg_{11w} \end{vmatrix}$$

11 = large seedlings remaining as large seedlings
ml = medium seedlings becoming large seedlings
mm = medium seedlings remaining medium seedlings
sm = small seedling becoming medium seedlings
ss = small seedlings remaining small seedlings
g_i = new small seedlings, germinated from depth i
mg; = loss from seedbank due to germination at depth i
$_w$ = time step used during the simulation of germination and early seedling development and survival is
1 week

$\mathbf{M}_k$ = transition matrices for survival of seedlings to mature weeds:

$$\mathbf{M}_k = \begin{vmatrix} 0 & s(\mathbf{p}_{2\text{-}4})_k & s(\mathbf{p}_{2\text{-}4})_k & s(\mathbf{p}_{2\text{-}4})_k & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & 0 & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & 0 & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 10 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{vmatrix}$$

$s(\mathbf{p}_{2\text{-}4})_k = a / [\, 1 + c * \text{total weed density}]$ (1)

$_k$ = refers to once during each season, about 11 weeks after planting

$\mathbf{B}_k$= matrices for the conversion from density of mature weeds to biomass:

$$\mathbf{B}_k = \begin{vmatrix} b(\mathbf{p}_1)_k & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 10 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 10 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 10 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 10 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 10 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{vmatrix}$$

$b(\mathbf{p}_1)_k = a / [\, 1 + c * \text{density of mature weeds}]$ (2)

$\mathbf{p}_1$ = density of mature weeds

$_k$ = refers to once during each season, about 11 weeks after planting

$\mathbf{N}_l$ = conversion matrices from weed biomass to number of seeds produced:

$$\mathbf{N}_l = \begin{bmatrix} sp(\mathbf{p}_1)_l & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$sp(\mathbf{p}_1)_l = a / [\ 1 + c * \text{biomass of mature weeds}]$ (3)

$_l$ = once a year at the end of each growing season

$\mathbf{S}_m$ = Survival matrices of seeds in and on the soil over one year:

$$\mathbf{S}_m = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & ss_{5\,m} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & ss_{6\,m} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & ss_{7\,m} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & ss_{8\,m} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & ss_{9\,m} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & ss_{10\,m} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & ss_{11} \end{bmatrix}$$

ss_i = annual seed survival rate at depth i

$_m$ = once a year in the spring before tillage, seedbed preparation and planting

$\mathbf{T}_n$ = transition matrices for vertical weed seed movement in the soil during tillage and seedbed preparation:

$$\mathbf{T}_n = \begin{vmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & t_{55n} & t_{65n} & t_{75n} & t_{85n} & t_{95n} & t_{105n} & t_{115n} \\ 0 & 0 & 0 & 0 & t_{56n} & t_{66n} & t_{76n} & t_{86n} & t_{96n} & t_{106n} & t_{116n} \\ 0 & 0 & 0 & 0 & t_{57n} & t_{67n} & t_{77n} & t_{87n} & t_{97n} & t_{107n} & t_{117n} \\ 0 & 0 & 0 & 0 & t_{58n} & t_{68n} & t_{78n} & t_{88n} & t_{98n} & t_{108n} & t_{118n} \\ 0 & 0 & 0 & 0 & t_{59n} & t_{69n} & t_{79n} & t_{89n} & t_{99n} & t_{109n} & t_{119n} \\ 0 & 0 & 0 & 0 & t_{5\,10n} & t_{6\,10n} & t_{7\,10n} & t_{8\,10n} & t_{9\,10n} & t_{10\,10n} & t_{11\,10n} \\ 0 & 0 & 0 & 0 & t_{5\,11n} & t_{6\,11n} & t_{7\,11n} & t_{8\,11n} & t_{9\,11n} & t_{10\,11n} & t_{11\,11n} \end{vmatrix}$$

t_{ij} = seeds moving from depth zone i to depth zone j

$_n$ = once a year in the spring before planting

APPENDIX B: ADDITIONAL INFORMATION ON SOURCES FOR PARAMETER ESTIMATES USED IN CHAPTER 3

Effects of depth of burial on seedling emergence

It was very wet in 1996, and rain water may have washed some seeds down within the soil profile and splashed seeds into the pipes from the surrounding field soil To prevent this from happening in 1997, plastic rings holding fine nylon mesh were placed directly under the seeds to prevent them from being washed down through the soil profile and pipe connector pieces were placed on top of the pipes to create a higher rim preventing seeds being splashed in or out of the pipes by intense rainfall.

Survival in rotation crops

Details to field study for crucifer survival, biomass production, and seed production in rotation crops:

In 1995 oat was planted at 108 kg ha^{-1} with 101 kg ha^{-1} NO_3NH_4, barley was planted at 134.5 kg/ha with 10 1 kg ha-' NO_3NH_4 and oat-pea-vetch was planted with 112 kg ha^{-1} pea, 34 kg ha^{-1} hairy vetch, both inoculated with the appropriate strain of Rhizobium and 54 kg ha" oat. In 1996 oat and barley were planted at 112 kg ha-' with 101 kg ha-' NO_3NH_4, and oat-pea-vetch with 185 kg ha^{-1} pea, 62 kg ha^{-1} oat, and 34 kg ha-' hairy vetch, inoculated with the appropriate strain of Rhizobium. No weed control measures were applied.

Survival in potato

1233 kg ha^{-1} 14: 14: 14 (N-P-K) was applied in a band next to the potato row at planting. In 1995 potato was planted on 3 1 May in 1996 on 3 June.

Seed survival

There are no published data on the survival of Brassica rapa seed in the soil. Some of the data published on Brassica kaber survival in the soil originates from seeds placed in nylon mesh bags. This method excludes seed predators and doesn't allow for cultivation, that would stimulate germination and therefore reduce seed survival. The seed survival data obtained from these studies consequently are likely to underestimate actual seed mortality in the field.

Donald (1993) buried B. kaber seeds 1.9 cm deep in mesh bags and recorded their survival over 4 years. He initiated the study twice in two consecutive years with seeds produced in the respective year. Seeds shed in year 1 decline much more in the first year of burial than in the following years, whereas seeds shed in year 2 decline almost linearly over time (Table A.1). Seeds used in study 1 matured under drought conditions. The fall after burial of study 1 had normal rainfall allowing for greater fall germination than in study 2, where drought conditions prevailed after burial. The differences in the survival curves could be the result of either one of these differences in environmental conditions. It can be expected that seed survival in agricultural fields subjected to tillage, cultivation and seed predation is lower.

Hails et al. (1997) studied the survival of B. kaber seed enclosed in nylon mesh-bags in a number of different habitats. All sites except for one were covered by perennial vegetation, either grassland or woodland, reducing the likelihood of B. kaber germination. In the one site, a fallow arable field, 60% of the seed survived one year and 58% two years. These survival rates were averaged over two burial depths (2 cm and 15 cm). Averaged over all sites 65% survived the first year of burial averaged over depth, and 58% survived at 2 cm and 72% at 15 cm depth. Under realistic conditions in an agricultural field lower survival would be expected, as the seeds would be exposed to conditions favoring germination more often, due to tillage and cultivation and a lack of vegetative cover.

Fewer B. kaber seeds survived in undisturbed soil after 10 years at 8 cm (30%) than at 30 cm depth (59%) in a study by Kolk (1962).

During periods of high germinability seeds in the soil show higher mortality that can only in part be accounted for by emergence (Donald, 1991; Donald, 1993). Seeds at shallower depths are more likely to be exposed to conditions that break dormancy and consequently are more likely to be lost from the seedbank either due to germination (successful or fatal) or decay than seed that remain dormant at greater depths in the soil.

A few studies investigated weed seed survival under cultivation. Warnes and Anderson (1984) studied the survival of B. kaber seed under field conditions with tillage operations over the course of 6 years by preventing new seed shed and sampling the soil seedbank to a depth of 30 cm annually (Table A.1). Their treatments with continuous wheat and annual fall tillage, either chisel or moldboard-plowing, were closest to the field conditions in the experiment used for validation of this model, i.e. under annual

crops and without the use of preemergence herbicides. However, the experiment used for validation was only tilled once every two years in the spring, not in the fall, and during the potato phase it received cultivations that did not occur in Wames and Anderson's study. Spring tillage allows the weed seeds to remain at the soil surface over winter where they are much more exposed to seed predation and unfavorable environmental conditions. Consequently seed survival in the study used to validate the model is likely to be lower than in the study by Wames and Anderson (1984). Losses of seeds lying on the soil surface can be high, for Avena fatua (L.) Wilson and Cussans (1975) found up to 75% seed loss during the post-harvest period. Wilson et al. (1984) assumed that loss for seeds on the soil surface is higher than for seeds covered by soil, because they are not protected from seed predators (Brust and House, 1988).

Table B.l. Seed survival rates of Brassica kaber in the soil.
Donald (1993) buried seeds 1.9 cm deep in mesh bags in two consecutive years. Seeds in study 1 matured under drought conditions, whereas seeds in study 2 matured in a season with normal rainfall. Wames and Anderson (1984) studied the survival of B. kaber seed under field conditions with tillage operations over the course of 6 years by preventing new seed shed and sampling the soil seedbank to a depth of 30 cm annually. Their fields were planted to continuous wheat with fall tillage (either chisel- or moldboard-plow).

Study year	survival rates 1	2	3	4	5	6	Source
1	0.46	0.48	0.40	0.14			Donald (1993)
2	0.83	0.69	0.31	0.17			Donald (1993)
	0.75	0.55	0.40	0.50	0.45	0.29	Wames and Andersen (1984)

Edwards (1980) found an average annual germination rate of 2.5% for B. kaber over the entire seedbank (all depths) in cultivated fields combined with the annual rate of decay of 17.9% (Kropac, 1966) the soil seedbank declines 20.4% annually, i.e. the annual survival rate averaged over all depths and seed ages is 0.80. This survival rate is very similar to the average annual survival rate from year 0 to year 3 of 0.74 in Warnes and Anderson's study (1984).

Cromar et al. (1999) estimated a rate of 82% seed predation of Echinochloa crus-galli seeds on the soil surface in the fall from the onset of seed rain to onset of snow cover (ca. 60 days). Invertebrate seed predators were responsible for most of the seed predation. However, Zhang (1993) found seeds of cruciferous species to be the least preferred by Harpalus rufipes (Carabidae) the dominant seed predator in potato fields in northern Maine (Zhang, 1993).

Additional References for Appendix:

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Zhang, J., 1993. Biology of Harpalus rufipes DeGeer (Coleoptera: Carabidae) in Maine and dynamics of seed predation. M.S. thesis, University of Maine, Orono.

BIOGRAPHY OF THE AUTHOR

Silke D. Ullrich was born in Freiburg i. Br., Germany, on May 14, 1964. She graduated from Kreisgymnasium Kirchzarten, Germany in 1983. She attended Albert-Ludwigs-Universität Freiburg, Germany and Trent University in Peterborough, Ontario, Canada and graduated in 1986 from Trent University with a Bachelor's degree in Biology. She returned to Freiburg and received her Diplom in Biology at Albert-Ludwig-Universtat Freiburg in 1990. After graduating she held several internships: on a biodynamic dairy and vegetable farm in France, with Ciba-Geigy in Switzerland in research in plant biochemistry and with 'The Research Institute for Biological Husbandry (FIBL) in Switzerland in an interdisciplinary cropping systems study. Then she worked as a research assistant in the School of Horticulture at the University of Western Sydney, Hawkesbury, Australia studying allelopathic effects of cruciferous crops on weeds.

She entered the Plant Science Doctor of Philosophy program at the University of Maine in 1994. During her graduate studies at the University of Maine she served as a graduate assistant in the Department of Plant, Soil and Environmental Sciences, as a research assistant leading a field study on the effect of soil management on interference between potatoes and common lambsquarters, served as field manager for the "Potato Ecosystem Project" and she taught weed ecology and management in the fall semester of 1999. After receiving her degree she will start postdoctoral work with USDA-ARS in Beltsville, Maryland. Silke is a candidate for the Doctor of Philosophy degree in Plant Science from The University of Maine in December, 2000.